INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

PROXIMATE AND ULTIMATE CONTROL OF REPRODUCTIVE EFFORT IN NORTHERN SHOVELERS (*Anas clypeata*) NESTING AT MINTO FLATS, ALASKA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

Margaret Christine MacCluskie, B.S., M.S.

Fairbanks, Alaska

August 1997

PROXIMATE AND ULTIMATE CONTROL OF REPRODUCTIVE EFFORT IN NORTHERN SHOVELERS (*Anas clypeata*) NESTING AT MINTO FLATS, ALASKA

By

Margaret Chistine MacCluskie

RECOMMENDED:

Advisory Committee Chair

Department Head

APPROVED:

Dean, College of Science, Engineering and Mathematics

Dean of the Graduate School

7-30-97

Date

Abstract - The purpose of this study was to examine factors that influence reproductive effort of female Northern Shovelers (*Anas clypeata*) nesting at Minto Flats, AK during summer 1991 - 1993. I investigated the importance of endogenous nutrient reserves to females during egg production and examined changes in organ weights and intestine lengths through the reproductive cycle. Changes in organ weights and intestine length were similar to those of shovelers nesting in Manitoba. Females used neither somatic lipid reserves, protein reserves, nor mineral reserves to produce eggs. Individual variation in somatic lipid reserves was explained by body size and nest initiation date, while variation in somatic protein reserves was explained by standardized nest initiation date. Somatic mineral variation was explained by differences among years. Neither somatic protein nor mineral reserves were reduced during incubation, but somatic lipid reserves decreased significantly. I conclude that endogenous nutrient availability does not proximately limit clutch size during laying for this population, possibly due to high productivity of interior Alaska wetlands and long days.

Little is known about nest attendance behavior of ducks in the subarctic; therefore, I examined shoveler nest attendance patterns at Minto Flats to determine if observed patterns differed from those documented for shovelers nesting in Manitoba, Canada. Shovelers nesting at Minto were less attentive and took more frequent, longer recesses than shovelers in Manitoba. I examined patterns of nest attendance during incubation in relation to clutch volume and female weight loss to determine if females

make tradeoffs between energy invested in the clutch and energy invested in incubation. I found no evidence of energetic tradeoffs by Shovelers nesting at Minto Flats.

To determine if the trait of synchronous hatching could limit clutch size for a species of the genus *Anas* I measured development time and metabolic rates of Mallard (*Anas platyrhynchos*) eggs incubated in a constant environment. Females varied in length of time their eggs required to reach the star-pipped stage of hatch. Metabolic rate of eggs varied positively with position in the laying sequence and varied among females. These results indicate that metabolic rate may act as a synchronization mechanism for hatch.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

PREFACE

Each chapter of this dissertation has been prepared for submission to a specific professional journal. Chapter 1 will be submitted to The Auk; Chapter 2 will be submitted to the Journal of Avian Biology; Chapter 3 will be submitted to Wildfowl, and Chapter 4 has been published (MacCluskie et al., The Condor 99:224-228). My co-author on the first 3 chapters is my Graduate Committee Chair, Dr. James Sedinger. His contribution to each chapter was in design of each study, suggestions for data analyses, and editing of manuscripts. Chapter 4 is co-authored with Dr. Paul Flint and Dr. Sedinger. Dr. Flint contributed to the genesis of that chapter, was involved with study design, data analysis and composition of the manuscript. Dr. Sedinger was involved in study design and editing of the manuscript. The 'we' in each chapter refers to myself and the coauthors for that chapter. However, the responsibility for any errors that may appear in any chapter of this dissertation are mine.

ACKNOWLEDGMENTS

Funding for this project was provided by U.S. Fish and Wildlife Service, Region 7, Migratory Bird Management, Alaska Department of Fish and Game, and Delta Waterfowl and Wetlands Research Station. Logistical support was provided by the Alaska Cooperative Fish and Wildlife Research Unit and the Institute of Arctic Biology. I am indebted to Rod King, U.S. Fish and Wildlife Service, Migratory Bird Management, for providing equipment and flying time as well as moral support. The Department of

Biology and Wildlife, University of Alaska Fairbanks provided teaching assistantships during my time as a graduate student. Many people served as field assistants at Minto Lake during data collection for this project: Greg Berger, Amy Larsen, Mike Petrula, Jon Rabley in 1991; Sarah Cheek, Amy Larsen, Brett Nelson, Tim Obritschkewitsch, Rick Studely in 1992; John Dunn, Mark Keech, Amy Larsen, and Tim Obritschkewitsch in 1993. The willingness of those people to work long and unusual hours when necessary was vital to the success of this project. Assistance with laboratory work was provided by Mike Eichholz, Delia Person, Brian Person, and Tawney Roberts. The work completed by these 4 people was the most tedious and in many ways the most difficult of the project, and their careful attention to detail during the entire process was appreciated. During 1994 data were collected at Delta Waterfowl and Wetlands Research Station and Julie Campbell, Lea Craig, Dean Jeske, and Kim Wright provided excellent assistance there.

Through the duration of this project discussion with other graduate students widened my perspective and contributed to the development of my thought. Mike Eichholz, Paul Flint, Mark Lindberg, Mark Herzog, Amy Larsen, Joel Schmutz, and Susan Sharbaugh provided lively and stimulating conversations.

I would like to thank my Graduate Committee, Dr. Brian Barnes, Dr. Pierre Deviche, and Dr. Robert White for their help with this thesis. They have given freely of their time and been supportive through the duration of this project. Special thanks go to

Dr. Jim Sedinger, my Committee Chair for his help over the last 6 years. He always made time to talk with me when I asked, and I have learned many things from him. He has made a significant contribution to my development as a scientist. Besides acting as my advisor at school, both he and his family welcomed us in their home during holidays and that was very much appreciated.

The last people I would like to thank were as important as any one else that assisted me with this project, although neither of these people were involved with data collection. My father, Jim MacCluskie, has provided vast support and love through this project, and his unshakable faith in me is a source of both comfort and motivation. My sister, Kathie MacCluskie, has spent many hours on the phone with me from across the country and has managed to make me laugh when I thought it was not possible. I am indebted to both of them and am very fortunate to have them for my family.

Finally, my thanks to my partner, Mark Lindberg. He motivates me both professionally and personally and has been with me through the daily struggles of this project for 6 years and life for the last 9 years. He has made it fun, exciting and worth every minute.

INTRODUCTION

The majority of studies examining breeding ecology of ducks have been conducted in mid-continental North America (the prairies). This region provides nesting habitat for some of the highest densities of nesting ducks in North America; however, similar densities of nesting ducks occur in interior Alaska, and little is known about factors affecting reproductive effort in those ducks. The term 'reproductive effort' in this study is used to indicate clutch size and clutch volume produced by a female and energy invested in incubation of eggs.

Previous researchers have found a positive correlation between the size of lipid reserves and clutch size in Snow Geese (*Chen caerulescens*). Snow Geese feed little during egg production; thus, this work provided evidence of proximal limitation of clutch size. Based on these results, numerous studies on the relationship between body reserves and egg production have been conducted for ducks which have been interpreted as providing evidence that nutrient reserves limited clutch size. Little attention has been paid to ultimate factors that may influence reproductive effort of female ducks. It has been proposed that egg viability and predation pressure could set the upper limit to clutch size for ducks. However, ultimate regulation of reproductive effort has not been rigorously tested. This study was designed to test proximate regulation of reproductive effort, but the potential role of ultimate regulation has been considered in interpretation of data.

Several studies have documented use of nutrient reserves during egg production and incubation for female ducks nesting in the prairies. Comparative studies among populations of the same species have not usually been conducted, yet, if there is variation in food abundance between two areas, then variation in nutrient reserve use by females could be observed. Two studies have been conducted on the influence of body reserves on clutch production in Northern Pintails (*Anas acuta*) (hereafter pintails) nesting in AK; however, there are no comparative data for Pintails nesting outside of Alaska. To assess the generality of patterns of nutrient reserve use for a population of ducks nesting outside the prairies, I determined patterns of nutrient reserve use in Northern Shovelers (*Anas clypeata*) (hereafter shovelers) nesting at Minto Flats, AK and compared these results to data from shovelers nesting in the prairies, in Chapter 1. Also in this chapter I documented changes in organ weights and intestine lengths and make comparisons to prairie-nesting shovelers.

Patterns of nest attendance have been documented for several species of Anatini, including Black Ducks (*Anas rubripes*), Common Goldeneyes (*Bucephala clangula*), shovelers, and Wood Ducks (*Aix sponsa*). However, little is known about incubation rhythms of subarctic nesting ducks and how these patterns compare to those of ducks nesting in the prairies. A further goal of this study was to determine how energy required by females to incubate clutches could modify reproductive effort. Chapter 2 reports nest attendance behavior of shovelers at Minto Flats and makes comparisons to data reported

for shovelers nesting in the prairies. Females may make energetic tradeoffs between energy they invest in clutch production and energy invested in incubating clutches. In Chapter 3 we examined this hypothesis by relating nest attentiveness to weight change during incubation and clutch volume produced.

Waterfowl typically produce one egg/day during egg-laying and initiate partial incubation before the clutch is complete. One result of this pattern of incubation is developmental asynchrony of eggs at the end of laying. However, eggs in a clutch generally hatch within 24 hours of each other, indicating that a mechanism exists which synchronizes hatch. Chapter 4 examines a specific mechanism by which hatch could be synchronized (i.e., variation in metabolic rates of eggs) and also evaluates whether the trait of synchronous hatching could limit clutch size in the genus *Anas*.

NUTRIENT RESERVE DYNAMICS AND REPRODUCTIVE INVESTMENT OF FEMALE NORTHERN SHOVELERS BREEDING AT MINTO FLATS, ALASKA.[1]

Abstract. We investigated the importance of endogenous nutrient reserves during egg production in a population of Northern Shovelers nesting at Minto Flats, AK. During the summers of 1991-1993 we collected 100 females to study organ dynamics and body composition through the reproductive cycle. Qualitatively, patterns of organ weights and intestine lengths changes during reproduction were similar to those of shovelers nesting in Manitoba (Ankney and Afton 1988), but absolute values differed. Shovelers in rapid follicle growth at Minto had larger hearts and livers and shorter intestines than prairie females. Similarly, laying females at Minto had significantly heavier hearts and shorter intestines than prairie females. To investigate the role of endogenous nutrient reserves in egg production, we used ANCOVA which included explanatory variables body size, nest initiation date and reproductive nutrient produced, for birds laying first clutches. Females did not use somatic lipid reserves, protein reserves or mineral reserves to produce eggs. Individual variation in somatic lipid reserves was explained by body size and nest initiation date; large females had larger lipid reserves and females that delayed nest

---

[1] Prepared for submission to *The Auk* as: MacCluskie, M. C. and J. S. Sedinger. Nutrient Reserve Dynamics and Reproductive Investment of Female Northern Shovelers Nesting at Minto Flats, AK.

initiation had smaller lipid reserves. Females increased somatic protein reserves for every day they delayed nest initiation, and somatic mineral variation was explained by differences among years. Neither somatic protein nor mineral reserves were used during incubation, but somatic lipid reserves decreased significantly. We conclude that endogenous nutrient availability does not proximately limit clutch size during laying for this population of Northern Shovelers, possibly due to the high productivity of interior Alaska wetlands and long days which allow females to forage extensively.

Key words: Anas clypeata, *clutch size, egg production, Northern Shoveler, nutrient reserves.*

INTRODUCTION

Lack (1968) proposed that for species with precocial young, including Anatidae, egg production is determined by nutrients available to females when they produce eggs. For arctic nesting geese, Ryder (1970) modified Lack's (1968) hypothesis to allow for use of previously stored somatic nutrients. Smaller body size of ducks precludes storage of sufficient endogenous reserves to produce the entire clutch (Afton and Paulus 1992). Nevertheless, Northern Shoveler (*Anas clypeata*) (hereafter shoveler) females nesting in the North American mid-continent use stored lipid reserves and store protein during egg production, which is associated with this species being an invertebrate specialist (Ankney and Afton 1988). Ankney and Alisauskas (1991) found that Gadwalls (*Anas strepera*), which are mainly herbivorous, used both somatic lipid and protein to produce eggs.

although lipid was used at a higher rate than protein. Nearly all studies of temperate-nesting ducks have detected use of stored lipid reserves during egg-laying (Krapu 1981, Drobney 1982, Ankney and Afton 1988, Alisauskas 1990, Barzen and Serie 1990, Afton and Ankney 1991, Ankney and Alisauskas 1991, Esler and Grand 1994). While several studies detected use of stored protein reserves during laying (Alisauskas and Ankney 1990, Ankney and Alisauskas 1991, Mann and Sedinger 1992, Esler and Grand 1994), in most cases protein was not utilized at as high a rate as lipid. Use of a somatic nutrient during egg production provides evidence that females are unable to acquire sufficient quantities of a nutrient from the environment to produce eggs. Use of lipid reserves, combined with a positive relationship between rapidly developing follicles and remaining lipid reserves, has been taken as support for the hypothesis that lipid reserves limit egg production in these ducks (Alisauskas and Ankney 1992), although recently this approach has been questioned (Sedinger et al. 1997).

Most studies addressing nutrient limitation during egg production of ducks have been conducted in the mid-continent region of North America (Krapu 1981, Tome 1984, Ankney and Afton 1988, Alisauskas et al. 1989, Afton and Ankney 1990, Ankney and Alisauskas 1991). Only two studies on an upland nesting species (Northern Pintails, *Anas acuta*) have been conducted on breeding populations outside the prairies (Mann and Sedinger 1993, Esler and Grand 1994). It has not been possible to assess the generality of patterns of nutrient reserve use for populations outside the prairie region because

comparable data have been lacking for populations of a single species both inside and outside this region.

It has been thought subarctic nesting ducks may have a greater difficulty meeting their energy requirements during egg production in comparison to mid-continent nesting females for the following reasons. First, ducks nesting in interior Alaska migrate relatively farther from wintering grounds (e.g., Louisiana, southern California, MacCluskie unpub. data) than temperate nesting ducks, thus requiring more energy to return to breeding areas. Second, at high latitudes time available for egg production and maturation of broods is reduced because of a shortened growing season. For example average date of ice breakup on water bodies in interior Alaska is 6 April and average onset of freezing temperatures is 2 September (Selkregg 1974). Third, primary production of subarctic wetlands has been assumed to be lower than that of temperate wetlands (MacLean 1978, Risser 1981), resulting in nutrients necessary for egg production being more difficult to acquire.

Despite the expectation that exogenous and endogenous nutrients might limit clutch size to a greater extent in the subarctic than at temperate latitudes, Shovelers nesting at Minto Flats, AK lay, on average, only 0.1 eggs less than their prairie- nesting counterparts (Petrula 1993). Our purposes in this study were to investigate patterns of nutrient reserve use by shovelers breeding in a subarctic wetland and to compare these results to previously published data for shovelers from the mid-continent (Ankney and

Afton 1988). If exogenous nutrients limit egg production in shovelers nesting at Minto Flats (hereafter Minto), then we predicted we would observe similar or greater nutrient reserve use by shovelers at Minto compared to those nesting in Manitoba (Ankney and Afton 1988).

METHODS

This study was conducted on the Minto Flats State Game Refuge (64° 50' N, 148° 50'W), AK during the summers of 1991-93 (see Mann and Sedinger 1993 for study area description). Shovelers at Minto Flats State Game Refuge arrive, on average, on 28 April and initiate nests from mid-May to mid-June (Petrula 1993).

Body Composition

We collected females beginning mid-May in each year (approximately 2 weeks before peak nest initiation) and continued collecting birds until most females in the study area had begun incubation. Each day we started at a randomly chosen location on the study area and opportunistically collected females as they were encountered. We collected randomly chosen females on nests late in laying and during incubation to complete the sample of breeding birds. When collected, females were weighed to the nearest 1.0 g and visually classified into one of four reproductive categories (non-Rapid Follicle Growth, Rapid Follicle Growth, laying, or incubating) based on ovarian characteristics (Ankney and Afton 1988). We defined females whose follicles did not contain yolk as not having initiated rapid follicle growth (non-RFG) (Ankney and Afton 1988). RFG females had at

least one yolky follicle but no postovulatory follicles, while laying females had at least one postovulatory follicle and one or more follicles in rapid development (Ankney and Afton 1988). Incubating females were collected from known nests based on candling (Weller 1956). Ovaries and oviducts were removed upon collection and placed in a 10% formalin solution for preservation until further analysis.

We measured the following morphological characters (± 0.1 mm) using vernier calipers: culmen length, culmen width at the widest point, body length from distal edge of culmen to end of pygostyle, wing chord, and tarsus. Carcasses were frozen after we removed reproductive organs.

In the laboratory we shaved and plucked carcasses to remove all feathers (Raveling 1979). Intestinal tracts were removed; intestine lengths were measured (± 0.5 cm), and intestines were stripped of contents and weighed. We removed hearts, gizzards, and livers, cleaned gizzards of contents, and weighed all organs (± 0.01 g). Carcasses, with all organs replaced, were homogenized in a meat grinder, and a 30 g aliquot was removed for composition analyses. We dried aliquots in an oven at 90°C to constant weight, extracted lipid from aliquots with petroleum ether using a Soxhlet apparatus (Dobush et al. 1985) for 24 hours, and determined mineral content by combusting samples in a muffle furnace (Ankney and Afton 1988). We estimated protein content of aliquots as the difference between dried, lipid-free aliquot weight and mineral weight. We calculated whole carcass composition (somatic lipid, hereafter S-lipid, and somatic

protein, hereafter S-protein) by multiplying the proportions of each nutrient in aliquots by the ingesta- and feather-free carcass weight (Ankney and Afton 1988).

Reproductive Organs - Ovaries from non-RFG birds were kept intact and analyzed for lipid, protein and mineral content using procedures described above. For laying birds, each yolky follicle was excised and analyzed separately for protein, lipid and mineral content (Ankney and Afton 1988). The remaining portion of the ovary, containing no yolky follicles, also was analyzed. Oviducts were removed, dried, and analyzed for nutrient content. To estimate nutrients committed to eggs by laying and incubating females we determined lipid, protein and mineral content of a sample of unincubated eggs (n = 32). We multiplied the number of postovulatory follicles in ovaries of laying and incubating females by the average mass of nutrients found in the sample of unincubated eggs. All components of the reproductive tract plus eggs already laid were added together to determine total nutrient commitment to reproduction (R-lipid, R-protein).

We assumed follicles damaged during collection had the same nutrient content as follicles at the same stage of development in a sample of birds with a complete set of developing follicles (Afton and Ankney 1991). To estimate the nutrient content of damaged follicles, we regressed g of nutrient from the largest follicle on the g of nutrient in the next largest follicle in the hierarchy. Corrective equations determined were: fat $_{follicle}$ = 1.5517 + 0.9838(fat $_{follicle-1}$); n = 8, r^2 = 0.77. Protein $_{follicle}$ = 0.10206 +

0.6334(protein $_{follicle-1}$): n = 8, r^2 = 0.6826.

Statistical Analyses

To control for variation in structural size among birds in nutrient reserve analyses, we computed Principal Component scores for each bird (Alisauskas and Ankney 1987) based on the correlation matrix for measurements of culmen, keel, tarsus, body length and wing chord (Ankney and Afton 1988). PC1 scores described 32% of total variance in the original data.

We examined variation in organ weights and intestine length among females from Minto in each reproductive class and compared organ dynamics between Minto and Manitoba birds using the General Linear Models procedure (GLM) of SAS (SAS Institute 1992). Reproductive classes (non-RFG, RFG, laying, incubating), year of collection, and the interaction between class and year were included in the model. PC1 score was also included as a continuous variable. If the interaction term was not significant it was excluded from the model, likewise, any main effect not contributing significantly to the model was also excluded. We used Least Square Means for each reproductive class from the GLM procedure and compared adjacent classes of birds using *t*-tests adjusted for the number of comparisons made using the GLM procedure (SAS 1992). To compare mean values of organ weights and intestine lengths between shovelers from Minto and Manitoba (Ankney and Afton 1988) we used RFG and laying birds only. Least Square Means from Minto birds were compared to mean values reported for Manitoba birds

(Ankney and Afron 1988) using *t*-tests adjusted for the number of comparisons.

To control for variation among females associated with laying date we calculated adjusted nest initiation dates (i.e., the first day an egg was laid in a nest) in each year for laying and incubating females by determining the day on which the greatest number of nests were initiated (peak nest initiation) from known nests in each year and adjusting date of nest initiation relative to that peak for each female collected. We also included this variable in all subsequent analyses.

To evaluate the contribution each somatic nutrient (lipid, protein, and mineral) made to reproduction, we used models in which somatic nutrient was the dependent variable and the independent variables were reproductive nutrient, year, nest initiation date, PC1; all possible 2-way interactions were initially included. The contribution of each variable was evaluated using Type III Sums of Squares. Interaction terms that did not contribute significantly to the model were eliminated.

We also used the method of Sedinger et al. (1997) to directly test the hypothesis that nutrient reserves regulated clutch size. This analysis was restricted to females late in laying for whom complete clutch size could be determined. We used an ANCOVA model for each S-nutrient (protein, lipid and mineral) with S-nutrient as the dependent variable, clutch size as a class variable, and standardized date of nest initiation and R-nutrient as covariates. A significant clutch size effect is evidence of nutrient limitation of clutch size (Sedinger et al. 1997).

Geographical differences in lipid and protein use by females were also compared using ANCOVA. We used a model with S-nutrient as the dependent variable, area of collection (Minto or Manitoba) as the class variable, and R-nutrient a covariate.

RESULTS

Organ Dynamics

We collected 100 females during the 3 years of the study: 46 in 1991, 30 in 1992 and 24 in 1993. We used only females producing their first nests of the year ($n = 41$) for analyses concerning egg production. There was no overall effect of reproductive category on heart weight of females (Table 1). Reproductive classes varied significantly in liver weight ($P < 0.001$). Liver weight was larger in RFG birds than in non-RFG birds ($t_{21\ df} = 2.67$, $P < 0.01$) and decreased from laying to incubation ($t_{72\ df} = 7.74$)(Table 1). We observed annual variation in gizzard and intestine weights. The overall model for gizzard weight was significant ($P < 0.001$), but the only significant difference between classes of birds was between laying and RFG females: laying females had significantly lighter gizzards than females in RFG ($t_{48\ df} = 2.22$, $P = 0.05$). Overall, intestine weight increased from Non-RFG to RFG ($t_{22\ df} = 2.20$, $P < 0.05$), did not change from RFG to laying, and declined significantly from laying to incubation ($t_{51\ df} = 7.00$, $P < 0.001$)(Table 1). Similarly, variation in intestine length was also significant among reproductive classes ($P < 0.001$). Length of intestines of incubating females were shorter than those of laying females ($t_{65\ df} = 7.29$, $P < 0.001$).

Females from Minto in both RFG and laying classes had significantly heavier hearts than birds from Manitoba (RFG $t_{33\ df} = 6.45$, $P < 0.001$, and laying $t_{73\ df} = 9.47$, $P < 0.001$)(Table 2). Mean liver weight was heavier for Minto females than for Manitoba females ($t_{34\ df} = 2.75$, $P < 0.01$) during RFG, while for laying females liver weight did not differ between the two areas. For all 3 years combined, neither gizzard nor intestine weights differed significantly between Minto and Manitoba. Mean intestine weight of laying Minto females in 1991, however, was significantly lighter than that of Manitoba females ($t_{57\ df} = 3.05$, $P < 0.01$). Similarly, intestine length of Minto females was shorter than that of Manitoba females during both RFG ($t_{34\ df} = 3.46$, $P < 0.01$) and laying ($t_{70\ df} = 3.65$, $P < 0.001$)(Table 2).

Egg Production

For RFG and laying birds ($n = 41$), somatic lipid reserves varied with standardized nest initiation date ($P = 0.007$) and body size ($P = 0.04$) (Table 3). Somatic lipid declined, on average, 0.85 ± 0.30 (SE) g for each one day delay in nest initiation. Slopes of the lines representing S-lipid use during egg production for Minto and Manitoba were significantly different ($F = 18.76$, df = 89, $P = 0.0001$) (Fig. 1). The adjusted y-intercept for Minto females was significantly lower than the y-intercept for Manitoba females ($F = 14.17$, df = 89, $P = 0.003$)(Fig . 1).

Somatic protein in RFG and laying females varied with standardized nest initiation date ($F = 3.98$, df = 41, $P = 0.05$)(Table 3). Females increased somatic protein

reserves by 0.63 ± 0.31 (SE) g of protein for each day they delayed nest initiation ($P < 0.001$). S-protein did not co-vary with R-protein ($F = 0.10$, df = 41, $P = 0.75$). Slopes of the lines representing S-protein dynamics for Minto and mid-continent nesting shovelers did not differ ($F = 1.21$, df = 89, $P = 0.27$): however, the adjusted y-intercept of Minto females was 15.47 ± 4.44 (SE) g above the y-intercept for Manitoba females and these intercepts are significantly different from each other ($F = 74.24$, df = 89, $P = 0.001$).

We observed annual variation in S-mineral reserves for our sample of birds (F = 30.36, df = 89, $P > 0.001$)(Table 3). No other variable included in our model explained variation in S-mineral. S-mineral did not co-vary with R-mineral. Slopes of lines describing changes in S-mineral with R-mineral between Minto and Manitoba are different ($F = 9.48$, df = 89, $P = 0.002$) and the adjusted y-intercept of Minto birds is 4.81 g above the Manitoba intercept ($F = 11.68$, df = 89, $P < 0.001$)(Fig. 1).

Clutch size explained no variation in S-lipid reserves ($F = 0.44$, $P = 0.80$) in our sample of late layers ($n = 17$), nor did clutch size, or standardized date of nest initiation. Likewise, clutch size explained no variation in S-protein reserves ($F = 0.67$, df = 16, $P = 0.66$) or S-mineral reserves ($F = 0.54$, df = 16, $P = 0.74$).

Incubation

Variation in somatic lipid for incubating females was best described by a model including day of incubation and standardized date of nest initiation. Lipid reserves declined 1.01 ± 0.36 (SE) g for each day of incubation ($F = 7.63$, df = 37, $P < 0.001$) and

0.86 ± 0.25 (SE) g for every day later the nest was initiated (F = 10.44, df = 37, P< 0.001). In contrast, a model including date of nest initiation and PC1 best described variation in somatic protein reserves during incubation. Somatic protein declined 0.48 ± 0.26 (SE) g for every day later a nest was initiated (F = 3.23, df = 36, P < 0.06), while somatic protein increased 3.56 ± 2.04 g for each unit increase in PC1 (F = 3.04, df = 36, P < 0.09). S-mineral also declined for each day later a female initiated her nest (0.19 ± 0.11 (SE) g) (F = 3.15, df = 36, P = 0.08). Slopes of lines relating lipid reserve dynamics to day of incubation did not differ between females from Minto and Manitoba (F = . df = 36, P = 0.75) (Fig. 2), although the adjusted y-intercept for Minto females was above the y-intercept for Manitoba females (Minto y-intercept = 65.36 g S-lipid, Manitoba y-intercept = 47.01 g S-lipid, F = 12.09, df = 49, P = 0.008)(Fig. 2).

DISCUSSION

Organ Dynamics

Hearts and livers of RFG and laying females were larger at Minto than Manitoba; however, intestine lengths of Minto females were shorter than those from Manitoba females (Table 2). Larger hearts of Minto females may be due to longer migrations necessitated by nesting in interior Alaska. Shovelers at Minto lay eggs that, on average, have more lipid than Manitoba females (Minto 5.28 ± 0.05 S.E. g, Manitoba 4.96 ± 0.12 S.E. g) ($t_{2.64\ df}$ = 2.46, P < 0.025). Thus larger livers in Minto females may be a result of producing eggs with more lipid.

Female shovelers nesting at Minto Flats undergo patterns of organ dynamics similar to Shovelers nesting in Manitoba (Ankney and Afton 1988), as well as prairie-nesting Ruddy Ducks (*Oxyurini jamaicensis*) (Tome 1984) and Mallards (*Anas platyrhynchos*) (Krapu 1981). Increased liver weight during RFG and laying likely is associated with yolk production (Sturkie 1986, Afton and Ankney 1988). Average intestine weight increased from the non-RFG to the RFG stage. This trend of increasing intestine weight during egg formation is consistent with the hypothesis that females increase gut capacity as nutrient intake increases (Ankney 1977, Drobney 1984, Ankney and Afton 1988).

The size of every organ measured (except gizzard) declined significantly from laying to incubation. We attribute these declines to reduced use and atrophy, not catabolism of muscle tissue to meet energy requirements, because females did not reduce protein reserves during incubation. If catabolism of organ tissue serves as a metabolic fuel for incubating females, we would expect to observe a significant decline in somatic protein during incubation.

Egg Production

We failed to detect a decline in either protein or lipid reserves in female shovelers as egg laying progressed. If availability of exogenous nutrients limited egg production of shovelers nesting at Minto, we would have observed declines in somatic protein and/or lipid levels during egg production. Thus female shovelers nesting at Minto contrast with

several other duck species, which reduce lipid reserves during egg production (see Alisauskas and Ankney 1992 for review, but see Tome 1984, Dobush and Ankney 1986, and Mann and Sedinger 1993). Our results showing neither storage nor use of any nutrient during egg production differ from female shovelers in Manitoba. Ankney and Afton (1988) reported that females stored protein at a significant rate of 0.10 g of S-protein for each g of R-protein made during egg production and used lipid during reproduction at a significant rate of 0.72 g of S-lipid for each gram of R-lipid produced ($P < 0.001$).

Additionally, we found no relationship between clutch size and any somatic nutrient reserves for females late in laying. Our observed lack of a relationship between somatic nutrients and reproductive nutrients is not consistent with a hypothesis of proximal limitation of clutch size by nutrient availability during egg production for shovelers nesting at Minto Flats. Differences in nutrient reserve dynamics between shovelers nesting in Manitoba and Minto indicate fundamental differences in nutrient balance during laying between females nesting in the 2 areas.

Several hypotheses could explain why nutrient reserve dynamics of Minto females differ from those of females nesting in Manitoba. Macroinvertebrate abundance in Big Minto Lake (the central area of collection in this study) is comparable to that of temperate lentic systems (Jacobs 1992). Additionally, from 20 May to 20 July, interior Alaska experiences approximately 22 hours of daylight. Therefore relatively high

secondary productivity rates coupled with long days may enable female shovelers to ingest greater quantities of nutrients daily, thereby remaining in energy and protein balance during egg production. However, we do not attribute the nutrient reserve use patterns we observe solely to available daylight because nonbreeding waterfowl are known to feed during nighttime in the contiguous 48 states (Tamisier 1974, Jorde 1981, Paulus 1984a, Paulus 1984b), and we believe it likely that females nesting in the mid-continent use moonlight to feed during the night. Additionally, if food was available in super-abundance for females at Minto, we might expect to observe protein and potentially lipid storage during egg production, and we did not. We suggest, however, that the combination of high primary productivity and long day length allows females to arrive at Minto and feed sufficiently to maintain energy balance.

Differences in patterns of nutrient reserve use between Minto and Manitoba might also be associated with differences in body size. Laying Minto females weighed more ($\bar{x}$ = 567.5 ± 10.1 g SE; $t_{2.69\,df}$ = 7.55, $P < 0.001$) than females from Manitoba ($\bar{x}$ = 516 ± 6 g SE), and RFG and laying females from Minto had larger amounts of somatic protein (ANCOVA $P < 0.001$.: Minto = 114.19 ± 1.93 g, Manitoba 99.3 ± 1.15 g; $t_{2.96\,df}$ = 14.28, $P < 0.001$). Lipid reserves increase with body mass to the 1.19 power (Lindstedt and Boyce 1984), while metabolic rate increases with lean body mass to the 0.734 power (Aschoff and Pohl 1970). Thus fasting endurance of females should increase with body mass to the 0.35 power and additionally, if food intake is proportional to body size, large

females would be more efficient at utilizing food resources. This may explain why females at Minto are less reliant of food reserves to produce eggs. To determine if females from Minto are structurally larger than females nesting in the prairies, a direct comparison of body size measures is required.

Differences in nutrient reserve use between our results and those of Ankney and Afton (1988) might have resulted partially from the fact that we controlled for date of nest initiation in our analyses. Ankney and Afton (1988) did not include date of nest initiation in their analyses, although controlling for date has become standard in more recent papers (Alisauskas and Ankney 1990, Ankney and Alisauskas 1991, Esler and Grand 1994). If there is a correlation between stage of reproduction and date of collection, failure to include date in analyses could make it appear that S-reserves are being used for reproduction, when in fact they are not.

Including date of nest initiation in analyses has not resulted in a consistent pattern among species. Date did not explain any variation in lipid or protein reserves for gadwalls during egg production (Ankney and Alisauskas 1991), whereas date explained a significant proportion of the variation in lipid and protein reserves for pintails nesting in subarctic Alaska (Esler and Grand 1994). Alisauskas and Ankney (1990) included date in their analyses of Ring-neck Ducks (*Aythya collaris*), but only for pre-RFG and pre-laying females. In that study, date explained variation in protein but not lipid reserves. Inclusion of date in analyses may be most important in highly seasonal breeding

environments where food availability varies strongly with date. When we omitted date from our analyses and ran each model as S-nutrient = R-nutrient + body size, we found that our models no longer explained a significant amount of variation for lipid and protein (P = 0.44, and 0.90, respectively) in S-nutrients. For both lipid and protein, model r^2's were greatly reduced (r^2 = 0.04 and 0.01, respectively with date removed from the analyses). Although annual secondary production at Minto is comparable to that of a temperate lentic system (Jacobs 1992), but temporal dynamics of macroinvertebrate production have not been studied; thus we do not know when the food supply of shovelers is most abundant. Females, on average, may be better able to remain in a constant energy balance if they nest later, but a delay in nest initiation at Minto could be more costly than a nest initiation delay in a temperate environment, because the time available for ducklings to reach fledging at Minto is shorter.

Regulation of Clutch Size

Our data are inconsistent with a hypothesis that clutch size is proximally limited by lipid, protein or mineral availability during egg production. Dynamics of nutrient reserves, therefore, differed from patterns reported for other temperate nesting species except Ruddy Ducks (*Oxyura jamaicensis*) (Tome 1984, but see Alisauskas and Ankney 1994) and White-winged Scoters (*Mellanitta fusca*) (Dobush 1986), and for subarctic nesting northern pintails (Mann and Sedinger 1993, Esler and Grand 1994). Our data are consistent with an hypothesis that clutch size of most females is limited by some ultimate

mechanism, but we cannot rule out some females being held below this optimum clutch size by nutrient availability.

Lipid reserves declined with each day of nest initiation delay, indicating an energetic cost to later nest initiation. An ultimate explanation of our results may be that there are seasonal tradeoffs for females with regard to reproduction (Drent and Daan 1980, Daan et al. 1990). Females that nest later may need fewer reserves to complete breeding because of increased food availability. However, ducklings from these females may experience reduced food availability because they hatch after peak invertebrate abundance. The cost to the female, then, is reduced duckling survival and corresponding reduced recruitment of her offspring to the population. In contrast 'high quality' females nest earlier because they can and their ducklings survive better than those of females nesting later.

Another explanation for regulation of clutch size for shovelers at Minto is a combination of proximate and ultimate factors. Alisauskas and Ankney (1992) have proposed that females exhibit evolved patterns of nutrient reserve use or storage in a manner that reflects food availability in an average year. Gene flow between a subarctic nesting population and a mid-continent population may result in females that are genetically predisposed to respond to food abundance in timing of nest initiation in the prairies. Increased availability of nutrients at high latitudes reduces the need of females to use stored nutrients during egg production. We do not know to what extent Minto and

contiguous North American populations of shovelers mix on wintering grounds, however it appears that shovelers nesting in interior Alaska migrate during winter to southern areas of both the Pacific and Central Flyways (Bellrose 1976).

Most studies examining control of clutch size in ducks have focused on proximal mechanisms acting on females during egg production. Our data join 2 other studies (Tome 1984, Dobush 1986) in providing evidence that in at least some populations, clutch sizes most females is not limited by nutrient availability and some ultimate regulation of clutch size must occur. We suggest a need for studies specifically designed to test for evidence of ultimate regulation of clutch size in ducks and we propose that energetics of incubation should not be ignored in such studies (Alisauskas and Ankney 1991).

ACKNOWLEDGMENTS

Funding for this study was provided by U.S. Fish and Wildlife Service, Region 7, and Alaska State Department of Fish and Game. The Alaska Cooperative Fish and Wildlife Research Unit and Institute of Arctic Biology and Rod King, Office of Migratory Bird Management, Region 7 provided logistical support. We thank J. Rabley, B. Nelson, G. Burger, M. Petrula, M. Keech, A. Larsen, and T. Obritskeweich for field assistance. Laboratory assistance was provided by M. Eichholz, B. Person, D. Person and T. Roberts. Reviews by B. Barnes and E. Murphy improved this manuscript.

LITERATURE CITED

AFTON, A. D. 1979. Time budget of breeding Northern Shovelers. Wilson Bull. 91:42-49.

AFTON, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82:132-137.

AFTON, A. D. AND C. D. ANKNEY. 1991. Nutrient-reserve dynamics of breeding Lesser Scaup: a test of competing hypothesis. Condor 93:89-97.

AFTON, A. D. AND S. L. PAULUS. 1992. Incubation and brood care in waterfowl. Pages 62-108 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], The ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

ALISAUSKAS, R. T. AND C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in American Coots. Auk 102:133-144.

ALISAUSKAS, R. T. AND C. D. ANKNEY. 1992. The cost of egg-laying and its relation to nutrient reserves in waterfowl. Pages 30-61 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], The ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis. in B. D. J. Batt et al. [eds.], The ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

ANKNEY, C. D. AND C. MACINNES. 1978. Nutrient reserves and reproductive

performance of female Lesser Snow Geese. Auk 95:459-471.

ANKNEY, C. D. AND A. D. AFTON. 1988. Bioenergetics of breeding Northern Shovelers: diet, nutrient reserves, clutch size, and incubation. Condor 90:459-472.

ARNOLD, T. W., F. C. ROHWER, AND T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. Am. Nat. 129:643-653.

ASCHOFF, J., AND H. POHL. 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29:1541-1552.

BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.

COOPER, J. A. 1978. The history and breeding biology of the Canada geese of Marshy Point, Manitoba. Wildl. Mongr. No. 16.

DAAN, S., DIJKSTRA, C. AND J. M. TINBERGEN. 1990. Family planning in the kestrel (Falco tinnunculus): the ultimate control of covariation of laying date and clutch size. Behavior 114:83-116.

DOBUSH, G. R., C. D. ANKNEY AND D. G. KREMENTZ. 1985. The effect of apparatus, extraction time, and solvent type on lipid extraction of Lesser Snow Geese. Can. J. Zool. 63:1917-1920.

DOBUSH, G. R. 1986. The accumulation of nutrient reserves and their contribution to reproductive success in the White-winged Scoter. M. Sc. Thesis. Univ. Guelph.

Ontario.

DRENT, R. H. AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

DROBNEY, R. D. 1980. Reproductive energetics of Wood Ducks. Auk, 97:480-490.

DROBNEY, R. D. 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. Condor 84:300-305.

DROBNEY, R. D. AND L. H. FREDRICKSON. 1985. Protein acquisition: a possible proximate factor limiting clutch size in Wood Ducks. Wildfowl 36:122-128.

DRENT, R. H. AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

JACOBS, L. L. 1992. Aquatic ecology of two subarctic lakes: Big and Little Minto lakes, Alaska. M.S. Thesis, University of Alaska Fairbanks, Fairbanks.

JORDE, D. G. AND R. B. OWEN. 1981. Winter and spring staging ecology of Mallards in south central Nebraska. M.S. Thesis, Univ. North Dakota, Grand Forks, N.D. 116 pp.

KERR, D.C., C. D. ANKNEY, AND J. S. MILLAR. 1982. The effect of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. Can. J. Zool. 60:470-472.

KRAPU, G. L. 1974. Feeding ecology of pintail hens during reproduction. Auk 91:278-290.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29-38.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

LINSTEDT, S. L. AND M. S. BOYCE. 1984. Seasonality, fasting endurance, and body size in mammals. Am. Nat. 125:873-878.

MACLEAN, S. F. 1978. The detritus-based ecosystem. Pages 411-457 in J. Brown, P.C. Miller, L. L. Tieszen, F. L. Bunnell [eds.]. An arctic ecosystem - The coastal tundra at Barrow, Alaska. Academic Press, NY.

MANN, F. E. AND J. S. SEDINGER. 1993. Nutrient reserve dynamics and control of clutch size in Northern Pintails breeding in Alaska. Auk 110(2):264-278.

MILLER, P.C., P. J. WEBBER, W. C. OECHEL AND L. L TIESZEN. 1980. Biophysical processes and primary production. Pages 66-101 in J. Brown, P. C. Miller, L. L. Tieszen and F. L. Bunnell [eds.]. The coastal tundra at Barrow, Alaska. Academic Press, NY .

PAULUS, S. L. 1984a. Activity budgets of nonbreeding Gadwalls in Louisiana. J. Wildl. Manage. 46:483-489.

PAULUS, S. L. 1984b. Behavioral ecology of Mottled Ducks in Louisiana. Ph.D. Diss., Auburn Univ., Auburn Ala. 139 pp.

PETRULA, M. J. 1993. Breeding biology of Northern Pintails in Interior Alaska. M.S. Thesis, University of Alaska Fairbanks.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada geese with special reference to control of reproduction. Auk 96:234-252.

RISSER, P. G., E. C. BIRNEY, H. D. BLOCKER, S. W. MAY, W. J. PARTON AND J. A. WIENS. 1981. The true prairie ecosystem. Academic Press, NY.

RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. Wilson Bull. 82:5-13.

SAS Institute Inc. 1992. SAS/STAT guide for personal computers, version 6 edition. SAS Institute Inc., Cary, N.C.

SELKREGG, L. L. 1974. Alaska Regional Profiles: Yukon Region. University of Alaska Fairbanks, Arctic Environmental Information and Data Center. Fairbanks, AK.

TAMASIER, A. 1974. Etho-ecological studies of teal wintering in the Camargue (Phone Delta, France). Wildlfowl 27:19-31.

TOME, M. W. 1984. Changes in nutrient reserves and organ size of female Ruddy Ducks breeding in Manitoba. Auk 101: 830-837.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. J. Wildl. Manage. 20:111-113.

Table 1.1. Changes in mean weight and length of selected organ metrics of female Northern Shovelers nesting at Minto Flats, AK.

Organ metric [a]	Non RFG	*P* [b]	RFG	*P*	Laying	*P*	Incubating
Heart wt.[c]	6.55 ± 0.34 *n* = 10	nc[e]	6.96 ± 0.33 *n* = 11	nc	6.75 ± 0.18 *n* = 36	nc	6.21 ± 0.18 *n* = 35
Liver wt.	16.21 ± 1.19 *n* = 9	***	20.41 ± 1.03 *n* = 12	ns	20.44 ± 0.60 *n* = 36	***	13.91 ± 0.60 *n* = 36
Gizzard wt.[d]	7.74 ± 1.69 *n* = 10	ns	10.40 ± 0.52 *n* = 12	*	9.15 ± 0.29 *n* = 36	ns	8.68 ± 0.28 *n* = 37
Intestine wt.[d]	10.75 ± 3.45 *n* = 10	***	23.06 ± 1.06 *n* = 12	ns	21.85 ± 0.59 *n* = 36	***	16.07 ± 0.57 *n* = 36
Intestine length	244.2 ± 8.52 *n* = 10	ns	261 ± 7.78 *n* = 12	ns	268 ± 4.69 *n* = 33	***	219 ± 4.77 *n* = 32

[a] Weights are in g, lengths are in cm, measurements are expressed as means ± 1 S.E.

[b] *P* is the probability that adjacent means differ by chance; ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

[c] All mass measurements are wet measurements.

[d] Means are Least Squares controlling for differences among years.

[e] Overall ANOVA was not significant, therefore *t*-tests among classes were not computed.

Table 1.2. Comparisons of organ weights and lengths of female Northern Shovelers nesting at Minto Flats, AK and Manitoba, Canada.

	RFG			Laying		
Variable	**Minto Flats**	***P***[c]	**Manitoba** $n = 22$	**Minto Flats**	***P***	**Manitoba** $n = 37$
Heart wt.[a,b]	7.0 ± 0.3 $n = 11$	***	5.26 ± 0.09	6.8 ± 0.2 $n = 36$	***	5.15 ± 0.08
Liver wt.	20.4 ± 1.0 $n = 12$	**	17.3 ± 0.5	20.44 ± 0.7 $n = 36$	ns	19.7 ± 0.4
Gizzard wt.[d]	10.4 ± 0.5 $n = 12$	ns	10.2 ± 0.3	9.16 ± 0.2 $n = 36$	ns	9 ± 0.2
1991	--	--	--	8.11 ± 0.2 n =20	**	9 ± 0.2
Intestine wt.[d]	23.1 ± 1.0 $n = 10$	ns	23.9 ± 1.1	21.9 ± 0.6 $n = 20$	ns	22.4 ± 0.7
1991	--	--	--	19.6 ± 0.7 $n = 16$	**	22.4 ± 0.7
Intestine length	261 ± 7.7 $n = 12$	**	292 ± 7	268 ± 4.7 $n = 32$	***	294 ± 5

[a] Weights are in g, lengths are in cm, measurements are expressed as means ± 1 SE.

[b] All mass measurements are wet measurements.

[c] P is the probability that adjacent means differ by chance; ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

[d] Means are Least Square means controlling for differences among years.

Table 1.3. ANCOVA results describing variation in nutrient reserves for RFG and laying females nesting at Minto Flats, AK. Nest initiation date is standardized within each year.

Model								
Dependent variable	***F***	***P***	r^2	**Intercept**	**Source**	**Estimate**	***F***	***P***
S-lipid (n = 41)	5.16	0.01	0.21	48.83 ± 2.66[a]	R - lipid	0.04 ± 0.15	0.08	0.78
					Body size	4.27 ± 2.04	4.37	0.04
					Nest initiation date	-0.86 ± 0.30	8.13	0.007
S-protein (n = 41)	2.10	0.14	0.10	111.96	R - protein	0.05 ± 0.16	0.10	0.75
					Body size	-0.83 ± 2.13	0.15	0.69
					Nest initiation date	0.63 ± 0.31	3.98	0.05
S - mineral (n = 41)	15.59	>0.001	0.69	19.21	R - mineral	0.32 ± 0.08	0.14	0.71
					Nest initiation date	-0.5 ± 0.10	0.33	0.57
					Body size	-0.23 ± 0.56	0.17	0.68
					Year		30.36	>0.001

[a] Parameter estimate ± 1 SE

Figure 1.1. Commitment of somatic nutrients (protein, lipid and mineral) during egg production for shovelers nesting at Minto (open squares, dashed lines) and Manitoba (closed circles, solid lines). The equations for Minto data are: S-protein = 111.82 + 0.60(Standardized nest initiation date; S-lipid = 48.83 + 4.23 (Body size) - 0.85(Standardized nest initiation date); S-mineral = 19.22 + 4.76(Year). Equations for Manitoba data (Ankney and Afton 1988) are: S-protein = 97.8 - 0.10(R-protein); and S-lipid = 63.0 - 0.72(R-lipid); S-mineral = 18.95 + 0.07(R-mineral).

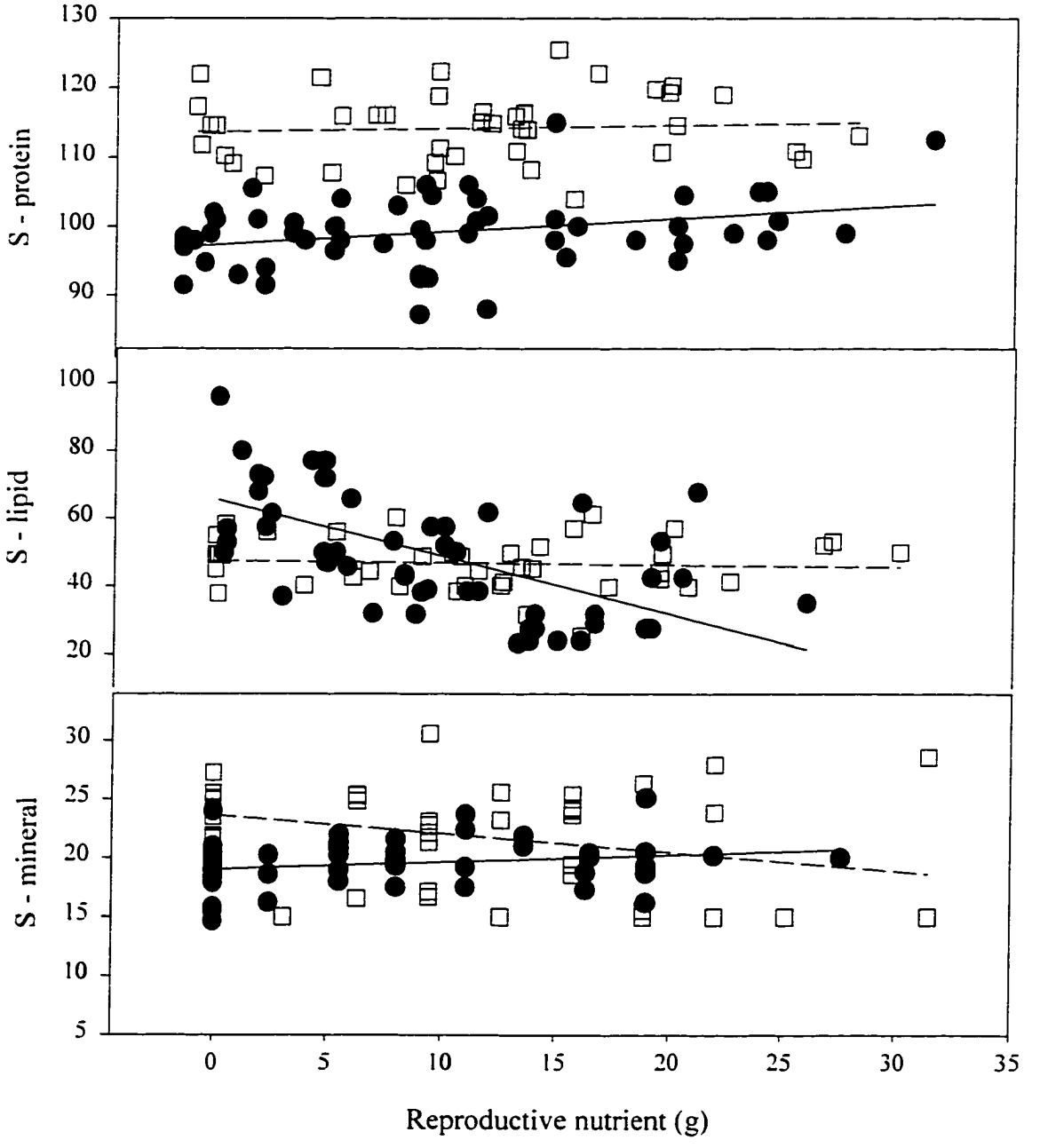


Figure 1.2. Use of somatic lipid during incubation by Minto females (open squares, dashed line) and Manitoba females(solid line). The equation for Minto females is S-lipid = 51.13 - 1.01(stage of incubation) - 0.86(standardized nest initiation date). The equation for Manitoba females is S-lipid = 44.8 - 1.68(day of incubation) (Ankney and Afton 1988).

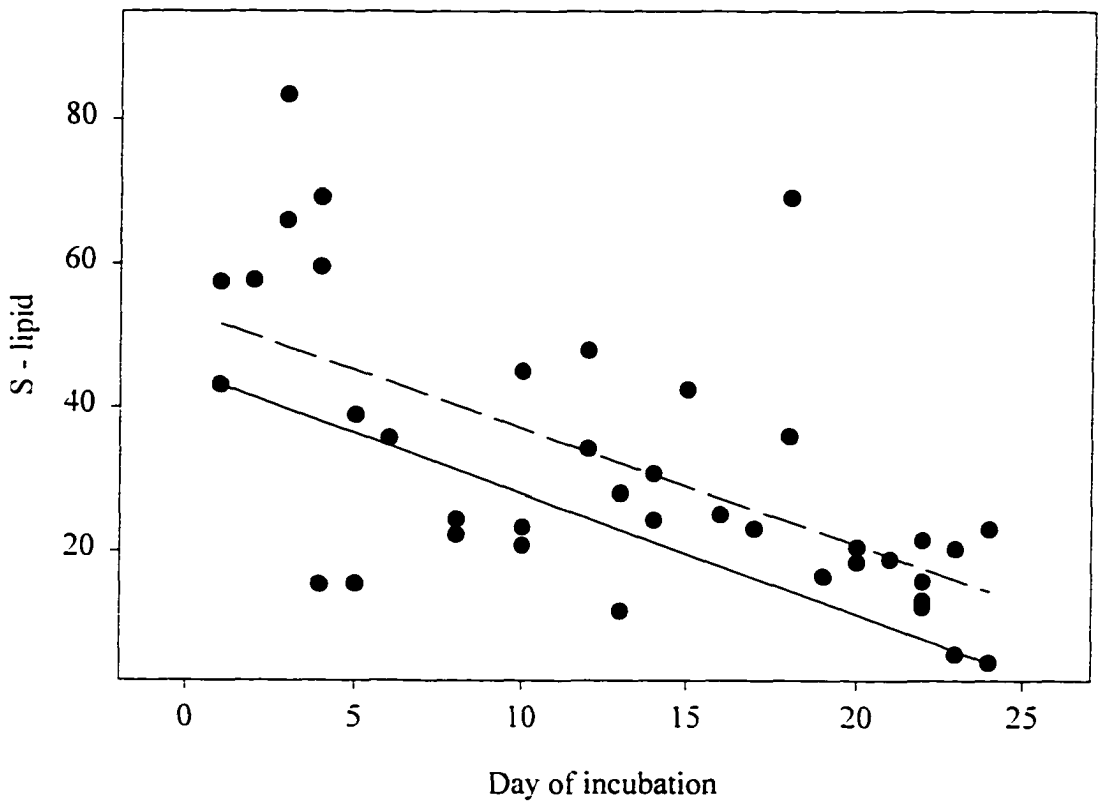
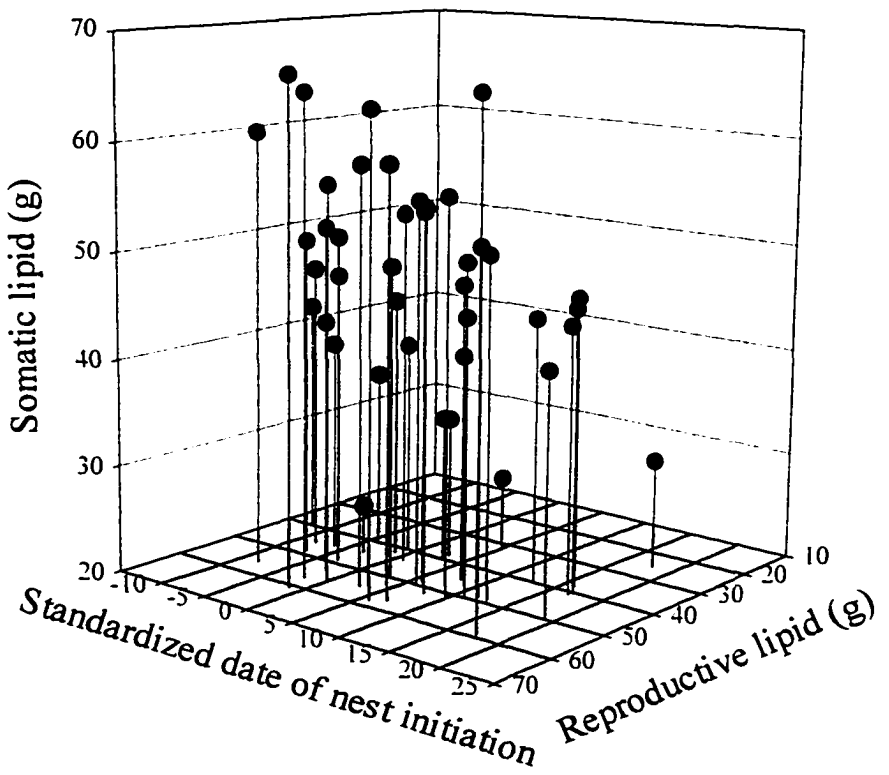


Figure 1.3. Use of somatic lipid during egg production by RFG and laying females at Minto. Somatic lipid values have been adjusted for body size based on ANCOVA results reported in Table 3.



Nest Attendance Patterns of Northern Shovelers (*Anas clypeata*) in the Subarctic [2]

Abstract. - We examined patterns of nest attendance of Northern Shovelers at Minto Flats, Alaska to determine if observed patterns differed from those documented for shovelers nesting in the mid-continent of North America. Data were collected on percent of time spent on the nest through incubation and nest temperatures for 15 females over 221 bird-days. Mean incubation constancy was 67 ± 0.16%. This value is significantly lower than mean constancy reported for Shovelers nesting in Manitoba and lower than values reported for all other *Anas* spp. Females nesting at Minto took twice as many recesses per day as did shovelers nesting in the prairies or other Anas species nesting in the prairies. Within the Minto sample, variation in percent of each day spent on the nest was explained both by variation among females and ambient temperature. Females spent less time on their nests each day as ambient temperatures increased. Females took more recesses per day as incubation progressed, but took fewer recesses as length of recesses increased. Females took longer recesses when ambient temperature was higher. Timing of recesses was similar to rhythms reported for shovelers in the prairies: most recesses were taken at mid-day, while fewer recesses were taken in the morning and evening.

---

[2] Prepared for submission to the Journal of Avian Biology as: MacCluskie, M. C. and J. S. Sedinger. Nest Attendance Patterns of Northern Shovelers (*Anas clypeata*) in the Subarctic.

Shovelers nesting at Minto Flats, AK spent less time on their nests during late evening and night than shovelers nesting in Manitoba; however, females responded to changes in ambient temperature in a similar manner. In light of data reported on nutrient reserve dynamics for this species nesting at Minto Flats our data provide support that females at Minto have more difficulty obtaining food resources during incubation rather than during egg production. Differences observed in attentiveness among females are likely related to variation in territory quality.

Keywords: incubation, Northern Shoveler, nest attentiveness, incubation constancy

Introduction

Patterns of nest attendance during incubation have been described for several species of Anatini, including Black Ducks (*Anas rubripes*)(Ringelman 1982), Common Goldeneyes (*Bucephala clangula*)(Mallory 1993), Northern Shovelers (*Anas clypeata*)(Afton 1980), and Wood Ducks (*Aix sponsa*) (Wilson 1985). However, little is known about incubation rhythms of subarctic nesting Anatini and how they compare to those of ducks nesting in the prairies. The purpose of this study is to compare incubation rhythms of Northern Shovelers (hereafter shovelers) nesting in the subarctic (Minto Flats, Alaska) to those of Shovelers nesting in the mid-continent of North America (Afton 1979), where breeding biology of most ducks has been studied.

Shovelers in both the subarctic and the prairies initiate nests midway through the

between earliest and latest nest initiating species (Petrula 1993, Afton 1980) and clutch size is similar between the two areas (9.2 for interior Alaska versus 10.0 for mid-continent North America, Petrula 1993). Also, recent evidence indicates that zooplankton, the primary food of shovelers (Swanson 1979, Krapu and Reinecke 1992), are similar in abundance in the 2 areas (Jacobs 1992). Environmental conditions differ between the 2 areas, however for example, the difference between mean daily maximum and minimum temperatures in Winnipeg, Manitoba is 40 - 50° C during May, June and July (Van Der Valk 1989) while the difference between daily mean maximum and minimum temperatures for the same months at Minto Flats (hereafter Minto) is 15 - 17° C (MacCluskie and Sedinger unpub. data). Mean daily temperatures at Minto range from 17.3° C in May to 20.5° C in July, while mean Winnipeg temperatures range from 11.3° C in May to 20.2° C in July. Also, Minto Flats experiences 22 hours of daylight beginning 20 May (Selkregg 1974), potentially providing greater opportunity for feeding.

Recent evidence suggests that female shovelers nesting at Minto may be structurally larger than females nesting in the prairies (MacCluskie 1997). We observed larger lean body mass in females collected from Minto Flats (MacCluskie 1997) compared to female Shovelers collected from Manitoba, Canada. Lipid reserves scale to body mass to the 1.19 power (Millar and Hickling 1990) while metabolic rate scales to body mass to the 0.734 power (Aschoff and Pohl 1972). Therefore, large females nesting at Minto are potentially able to carry absolutely more lipid reserves to sustain them

through incubation. Minto females might be able to be more attentive to nests because they have larger reserves.

Given these differences between females nesting in the two areas, we made predictions about incubation rhythms we expected to observe in females nesting in interior Alaska. First, we predicted that females in the subarctic would exhibit higher overall incubation constancy in comparison to females in the prairies, because, while food is equally abundant between the 2 areas and females at Minto have continuous daylight for feeding, rate of endogenous lipid reserve use during incubation is similar between females nesting at Minto and in Manitoba, Canada (MacCluskie and Sedinger, in review). Also because the range of temperatures experienced each day is smaller in interior Alaska than in the prairies, females nesting at Minto are not forced to remain on nests for long periods of time to protect eggs from either freezing or overheating (Webb 1987, Gloutney 1996). Overheating of eggs is particularly important because embryos that are overheated exhibit higher rates of deformity and death than embryos that are exposed to freezing temperatures (Webb 1987). Gloutney and Clark (1996) have suggested that protection of eggs from solar insolation during incubation imposes a significant energetic cost in Blue-winged Teal (*Anas discors*) females, and they also reported ground level temperatures during the breeding season that were below lower critical temperatures of Mallards (*Anas platyrhynchos*) and Blue-winged Teal 23% and 55% of the time, respectively. Thus daily temperature fluctuations experienced by females may play an important role in

determination of incubation constancy.

Second, we predicted that timing of recesses through the day should be more evenly distributed in the subarctic because the relatively low daily temperature range would release females from having to protect eggs from intense heat (Gloutney and Clark 1996, Afton and Paulus 1992) and from extreme cold (Caldwell and Cornwell 1975, Afton and Paulus 1992). Also continuous daylight may reduce the advantage of leaving the nest at a particular time to avoid predators (Afton and Paulus 1992, Hohman 1986).

Characteristics of recesses (recess duration and frequency) may be influenced by factors such as microclimate of the nest and weather (Afton and Paulus 1992). Northern Shovelers in the prairies and Snow Geese (*Anser caerulescens*) on Wrangel Island take fewer and shorter recess when ambient temperatures are low (Afton 1977, Krechmar and Syroechovsky 1978). This behavior is likely to reduce egg cooling and the associated longer embryo development time (Caldwell and Cornwell 1975), and females must expend more energy to rewarm a clutch at lower temperatures (Drent 1975). Thus females must balance their energetic requirements with conditions that are most favorable to egg development. We predicted that shovelers nesting in the subarctic would take more and relatively longer recesses when ambient temperatures were warm. We also predicted females nesting in the subarctic would take many short recesses during incubation, rather than few long recesses. Because daily maximum temperatures are not as high in the subarctic, Shoveler recesses should be timed primarily to minimize egg

cooling and energy required to rewarm a clutch.

Methods

We conducted this study during the summer of 1993 on Minto Flats, AK (64° 50' N, 148° 50'W). This area has been described in detail by Petrula (1993) and Mann and Sedinger (1992). Shovelers nesting in this wetland complex used meadow habitat dominated by bluejoint grass (*Calamagrostis canadensis*), sedge (*Carex sp.*), and marsh five-finger (*Potentilla palustris*). Average date of nest initiation (i.e., the first day an egg is laid) by shovelers was 30 May and the interval between initiation of the first and last nests was 40.0 ± 5.5 (S.D.) days (Petrula 1993). We initiated field work on 15 May and conducted standard searches for nests (Klett et al. 1986) from 0800 to 1400 hrs Alaska Daylight Time (ADT) each day. Nests were located when females were flushed from their nests. We individually numbered eggs and determined stage of incubation by candling eggs (Weller 1956).

We placed an artificial egg in the center, bottom of each nest for monitoring both nest attendance and nest temperature. Artificial eggs were composed of auto-body filler and housed a thermistor probe, an in-line microswitch and a 10,000 ohm resistor. The thermistor was connected to a single-channel data logger (OnSet Computer Corp.) which recorded the temperature of the thermistor. For a more detailed description of the device, computer program, and equations for temperature transformation see Flint and MacCluskie (1995).

We recorded data every 4.8 minutes, which minimized the number of visits required to download data and still allowed adequate detection of changes in nest temperature. Nests were revisited every 6 days at which time the full datalogger was removed and an empty datalogger was connected to the thermistor. This process required approximately 10 minutes. While we were at the nest site artificial eggs were checked for proper operation and eggs were recandled to check embryo development. After the initial nest visit we timed revisits to nests when females were least likely to be present, which we determined from the first 6 days of nest attendance data. At some nests (n = 6) we could not put artificial eggs in during the initial visit, and we returned to those nests and put in artificial eggs after 1400 ADT hrs to minimize disturbance to the female (Klett et al. 1986, Gloutney et al. 1993). If a female was flushed from her nest during a visit, we eliminated data from that hour and the following 2 hours from attendance records.

We used thermistor probes and single-channel dataloggers (OnSet Computer Corp.) to record ambient temperature data at nests. Ambient temperature thermistor probes were affixed to a piece of vegetation at the height of the top edge of the nest bowl and adjacent to the nest using a small plastic tie. Ambient temperature data were also recorded at 4.8 minute intervals and dataloggers were downloaded at the same time artificial egg dataloggers were downloaded. Data from ambient probes were used to determined an average hourly temperature, mean daily ambient temperature and daily maximum and minimum temperatures.

Calculations of nest attendance and incubation rhythms were based on the time females were present on nests after we eliminated disturbance of females due to observer influence. We defined resettlements of females on their nests, as opposed to incubation recesses, as occurring if we recorded female absence for less than 14.4 minutes and nest temperature declined <2° C. These criteria, therefore, provided a conservative estimate of time spent off the nest.

We calculated incubation constancy for each female as the total percent of the incubation period spent on the nest. We determined daily attentiveness as the percent of each day a female was on the nest, relative to the amount of time each day a nest was monitored. We calculated daily attentiveness in this manner to eliminate observer disturbances to nests and short term failure of dataloggers. To compare average incubation constancy and incubation rhythms of female shovelers nesting at Minto Flats to those for females nesting in the prairies (Afton 1980) and females of other *Anas* species we tested for differences between means using 2-tailed *t* - tests adjusted for the number of comparisons being made.

We used ANCOVA models to test hypotheses about variation in percent of day spent on nest, frequency of recesses, duration of recesses, and timing of recesses. In the most general models, we included all explanatory variables and all subsets of 2-way interactions, and then eliminated variables or interaction terms that did not explain a significant amount of variation in dependent variables using Type III Sums of Squares

(SAS 1992) and a corresponding significance value of 0.10. To model percent of each day a female spent on the nest, our initial model included individual female as a class variable, mean ambient temperature and day of incubation as covariates and all 2-way interactions. Length of recesses was modeled with ambient temperature and day of incubation as covariates, females and time of day the recess was initiated (time of day was divided into 4 classes of 6 hrs each) as class variables, and all 2-way interactions. Our model for variation in number of recesses taken per day included female as a class variable, while the covariates were ambient temperature, day of incubation, average length of recesses, and all 2-way interactions.

To determine if recesses were evenly distributed through the day, we first tested to determine if data from all females could be pooled. We performed separate χ^2 Goodness of Fit tests on each female for the time of day recesses were initiated (each day was divided into 4 6-hour time periods. Those values were combined and tested for heterogeneity among females (Zar 1984). If the null hypothesis of homogeneity among females in timing of recesses was not rejected data were pooled. The pooled data were then tested from departure from a uniform frequency of recesses among time periods using a χ^2 Goodness of Fit test.

Results

We monitored 14 female Shovelers for a total of 221 bird-days during our study. We recorded hourly and daily ambient temperatures at 1 to 7 nests during each day of the

study. Mean incubation constancy of shovelers nesting at Minto was significantly lower than shovelers nesting in Manitoba ($t_{24\ df} = 12.70$, $P < 0.001$)(Table 1). Consistent with lower incubation constancy, Minto females took more recesses per day during incubation ($t_{24\ df} = 4.74$, $P < 0.001$) and longer recesses than prairie nesting females ($t_{24\ df} = 9.67$, $P < 0.001$) (Table 1).

Female shovelers at Minto varied in the proportion of each day they spent on nests ($P < 0.001$), and females decreased their nest attendance by 0.7% (10.1 minutes per day) for each degree increase in ambient temperature ($P = 0.06$) (Table 2). Females varied in the number of recesses they took each day ($P = 0.0001$), and they took 0.05 ± 0.02 (S.E.) more recesses per day as they progressed through incubation ($P = 0.03$) (Fig. 1). As the number of recesses/day increased, mean length of recesses declined 0.002 ± 0.00006 (S.E.) minutes/day (Table 2). Variation in recess length was explained by variation among females, day of incubation and the interaction between female and day of incubation ($P = 0.0008$) (Table 2). Overall, females tended to take recesses that were 1.11 ± 5.56 (S.E.) minutes longer for each day they progressed through incubation ($P = 0.12$). However the interaction between stage of incubation and female was significant (Table 2) indicating that females did not increase recess lengths at the same rate as incubation progressed. Of the females studied, 8 females took shorter recesses for every day they progressed through incubation and 6 females took longer recesses as they progressed through incubation. Timing of recesses was not random through the day (χ^2_3

= 60.50). Fewer than expected recesses were taken between 0000 and 0500 hrs and more than expected were taken between 1200 and 1700 hrs (Fig. 2).

Discussion

Total incubation constancy and nest attendance patterns were different between Shovelers nesting at Minto and females nesting in the mid-continent of North America. Females nesting at Minto Flats were less attentive than females nesting in the mid-continent of North America. Correspondingly, the number of recesses each day and duration of recesses taken by shovelers at Minto were greater than for shovelers in Manitoba. Our prediction that females nesting at Minto would exhibit higher total incubation constancy was supported.

Females at Minto may be less attentive to their nests because of declining food abundance during incubation. Gizzard weight of incubating females does not decrease through incubation (MacCluskie and Sedinger, in review), which indicates females spend time feeding during incubation recesses as the gizzard serves as the primary site of food masceration in ducks (Sturkie 1976). Decline in gizzard weight is well documented in Anatids that feed little during incubation (Cantin et al. 1974, Milne 1976, Ankney 1977, Korschgen 1977, Raveling 1979). Afton (1979, 1980) predicted that the relationship between body size and fasting endurance was important in the evolution of incubation behavior. Afton (1979) also reported that females on recesses spent the majority of their time feeding. We do not have behavioral observations of females at Minto Flats during

recesses. During incubation shovelers at Minto use endogenous lipid reserves (MacCluskie 1997) at a rate equivalent to shovelers nesting in Manitoba (Ankney and Afton 1988). These findings suggest there may be seasonal differences between Minto and Manitoba in the timing of food availability relative to nesting for this species shovelers. Female shovelers at Minto do not use endogenous reserves to produce eggs, indicating that nutrients in food are adequate to meet nutritional needs during egg production, but deplete endogenous reserves during incubation, suggesting that food is in short supply at this time. In contrast, shovelers in Manitoba used stored reserves for both egg laying and incubation (Ankney and Afton 1988).

Daily timing of recesses for shovelers in Alaska differs from those reported for female Shovelers in the prairies where females take no recesses between 2200 and 0100 hrs CST (Afton 1979). Constant attendance during the night is thought to occur as a predator deterrent and to prevent eggs from cooling (Afton and Paulus 1992). Black ducks take recesses only during daylight hours (Ringelman and Longcore 1982), wood ducks begin spending the entire night on nests during laying (Wilson and Verbeek 1995), and common goldeneyes never left nests between 2000 and 0700 hours (Mallory and Weatherhead 1993). While hour of recess initiation was not evenly distributed through the day, shovelers at Minto took many recesses during the coolest parts of the day. Because ambient temperatures are not as cool at 'night' at Minto Flats in comparison to the prairies (Van Der Valk 1989), eggs would not cool as quickly at Minto Flats, making

nighttime recesses less energetically costly in terms of rewarming the clutch.

Risk of nest predation may be lower at night for females nesting at Minto in comparison to prairie-parkland nesting females. Waterfowl nesting in the prairie-parklands are subject to more and diverse mortality agents than species nesting elsewhere (Sargeant and Raveling 1992). The predator community of the prairie-parkland includes coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*), racoons (*Procyon lotor*), red foxes (*Vulpes fulva*), and American crows (*Corvus brachyrhyncos*) (Sargeant and Raveling 1992). The predator community at Minto consists primarily of Common Ravens (*Corvus corax*), red foxes, ermine (*Mustela erminea*), and peregrine falcons (*Falco peregrinus*) (Petrula 1993, MacCluskie and Sedinger, unpub. data). Our observed patterns of incubation recesses may partially be a result of essentially continuous daylight which reduces the advantage of females taking recesses during a particular time because predators are capable of hunting at all times.

Although daily rhythms of incubation are different between Shovelers nesting at Minto and Shovelers nesting in the prairie-parkland, females from the 2 areas responded similarly to changes in ambient temperature. As ambient temperatures increase, females increase the time they spend off nests. However females in Manitoba took very few recesses between 1000 and 1300 hrs, which is the hottest portion of the day (Afton 1980). In contrast, females at Minto took many recesses during the same time interval (Fig. 2). During this study, daily maximum temperature averaged 28.2°C and the daily minimum

averaged 11.3°C at nest bowls. Lethal effects of insolation may be rarely attained in interior Alaska, and females may take advantage of warm temperatures when nests cool at slower rates to maximize recess length and/or frequency.

Among-female variation we observed in percent of day spent on nest, number of recesses/day, and length of recesses may be a result of territory quality, female condition or both. We did not assess quality of individual territories of females in our study. However, females at Minto are in negative energy balance during incubation (MacCluskie and Sedinger, in review); thus poor territory quality could force some females to spend more time off their nests feeding to reduce negative energy balance. We are unaware of any studies addressing variation in quality of territories of shovelers.

We suggest that to explain reproductive patterns observed in the wild (e.g., clutch size, incubation behavior) it is necessary to examine all portions of a reproductive attempt. That is, incubation behavior must be evaluated not only with respect to variables measured during incubation, but also body condition and stresses experienced by females during egg production (Ankney and Alisauskas 1992, Afton and Paulus 1992). Such studies are difficult to conduct, but they are likely necessary to fully understand observed reproductive behavior.

Acknowledgments

Funding for this project was provided by Delta Waterfowl and Wetlands Research Station, Alaska Department of Fish and Game and U.S. Fish and Wildlife Service.

Region 7. Field assistance was provided by M. Keech, A. Larsen, T. Obritschkewitsch, and J. Dunn. B. Barnes and E. Murphy provided helpful review of this manuscript.

Literature Cited

Afton, A. D. 1979. Time budget of breeding Northern Shovelers. Wilson Bull. 91:42-49.

Afton, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82:132-137.

Afton, A. D., and S. L. Paulus. 1992. Incubation and brood care in waterfowl, p. 62-108. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. The ecology and management of breeding waterfowl. University of Minnesota Press. St. Paul.

Alisauskas, R. T. and C. D. Ankney. 1992. The cost of egg-laying and its relation to nutrient reserves in waterfowl, p. 30 -61. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. The ecology and management of breeding waterfowl. University of Minnesota Press. St. Paul.

Arnold, T. W., M. G. Anderson, R. B. Emery, M. D. Sorenson, and C. N. deSobrino. 1995. The effects of late-incubation body mass on reproductive success and survival of Canvasbacks and Redheads. Condor 97:953-962.

Aschoff, J., and H. Pohl. 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29:1541-1552.

Cantin, M., J. Bedard, and H. Milne. 1974. The food and feeding of Common Eiders in the St. Lawrence estuary in summer. Can. J. Zool. 52:319-334.

Delehanty, D. J. and L. W. Oring. 1993. Effect of clutch size on incubation persistence in male Wilson's Phalaropes (*Phalaropus tricolor*). Auk 110:521-528.

Duke, G. E. 1986. Alimentary canal: anatomy, regulation of feeding, and motility. Pp 529-555 *In* P. D. Sturkie [ed.], Avian physiology, 6th edition. Springer-Verlag, New York.

Flint, P. L. and M. C. MacCluskie. 1995. A device for simultaneously measuring nest attendance and nest temperature in waterfowl. J. Field Ornithol. 66:515-521.

Gloutney, M. L. and R. G. Clark. 1991. The significance of body mass to female dabbling ducks during late incubation. Condor 93:911-816.

Gloutney, M. L., R. G. Clark and A. D. Afton. 1993. Timing of nest searches for upland nesting waterfowl. J. Wildl. Manage. 57(3):597-601.

Gloutney, M. L., N. West, and R. G. Clark. 1996. Metabolic costs of incubation and clutch size determination in the Red Junglefowl, *Gallus gallus spadiceus*. Comp. Biochem. Physiol. 114A(3):265-270.

Hohman, W. L. 1986. Incubation rhythms of Ring-necked Ducks. Condor 88:290-296.

Kennamer, R. A., W. F. Harvey and G. R. Hepp. 1990. Embryonic development and nest attentiveness of Wood Ducks during egg laying. Condor 92:587-592.

Klett, A. T., H. F. Duebbert, C. A. Faanes, and K. F. Higgins. 1986. Techniques for

studying nest success of ducks in upland habitats in the prairie pothole region. U. S. Fish and Wildl. Ser. Res. Publ. No. 158. 24 pp.

Korschegen, C. E. 1977. Breeding stress of female eiders in Maine. J. Wildl. Manage. 41:360-372.

Krapu, G. and K. J. Reinecke. 1992. Foraging ecology and nutrition. Pp. 1-29 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. The ecology and management of breeding waterfowl. University of Minnesota Press. St. Paul.

Krechmar, A. V. and E. V. Syroechkovsky. 1978. Ecology of incubation in *Anser caerulescens* on the Wrangel Island. Zool. Zh. 57:899-910.

χ2 MacCluskie, M. C. 1997. Proximate and ultimate control of reproductive effort in Northern Shovelers (*Anas clypeata*) nesting at Minto Flats, Alaska. Ph.D. Thesis. University of Alaska Fairbanks, Fairbanks, AK.

Mallory M. L. and P. J. Weatherhead. 1993. Incubation rhythms and mass loss of Common Goldeneyes. Condor 95:849-859.

McKinney, F. 1973. Ecoethological aspects of reproduction. Pp. 6-21 *in* Breeding Biology of birds (D. S. Farner, ed.). Natl. Acad. Sci., Washington, D.C.

McKinney, F. 1975. The evolution of duck displays. Pp. 331-357 *in* Function and evolution of behavior (G. Barends, C. Beer and A. Manning, eds.). Clarendon Press, Oxford.

Milne, H. 1976. Body weights and carcass composition of the Common Eider. Wildlfowl 27:115-122.

Millar, J. S. and G. J. Hickling. 1990. Fasting endurance and the evolution of mammalian body size. Functional Ecology 4:5-12.

Raveling, D. G. 1979. The annual cycle of body composition in Canada Geese with special reference to the control of reproduction. Auk 96:234-252.

Ringelman, J. K., J. R. Longcore, and R. B. Owen. 1982. Nest and brood attentiveness in female Black Ducks. Condor 84:110-116.

Sargeant, A. B. and D. G. Raveling. 1992. Mortality during the breeding season. Pp 396-422 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], The ecology and management of breeding waterfowl. University of Minnesota Press. St. Paul.

Webb, D. R. 1987. Thermal tolerance of avian embryos: a review. Condor 89:874-898.

Weller, M. W. 1956. A simple field candler for waterfowl eggs. J. Wildl. Manage. 20:111-113.

Wilson, S. F. and N. A. M. Verbeek. 1995. Patterns of Wood Duck nest temperatures during egg-laying and incubation. Condor 97:963-969.

Table 2.1. Mean incubation constancy, mean number of recesses per day and recess duration for female Northern Shovelers nesting at Minto Flats, AK, Manitoba, Canada (Afton 1980), and all *Anas* spp. combined (Afton and Paulus 1992). Values are ± 1 S. E..

Parameter	**Minto Flats, AK** $n = 14$	**Manitoba, Canada** $n = 12$	**All *Anas* spp.** $n = 11$ **species, 16 studies**
Mean incubation constancy/day	67.0 ± 0.1	84.6 ± 0.5	86 ± 1.4
Mean number of recesses/day	4.1 ± 0.1	2.3 ± 0.1	2.2 ± 0.2
Mean recess duration (min.)	110 ± 11.2	93 ± 2.9	88 ± 10

Table 2.2. ANCOVA results describing variation in selected incubation behavior parameters for Shovelers nesting at Minto Flats, AK, 1993.

Model								
Dependent variable	***F***	***P***	r^2	**Intercept**	**Source**	**Estimate**	***F***	***P***
% of day on nest (n = 198)	3.72	0.0001	0.23	0.962 ± 0.09[a]	Female (df = 13)	-	3.84	0.0001
					Ambient temp. (df = 1)	-0.007 ± 0.004	3.50	0.06
# recesses per day (n = 204)	6.54	0.0001	0.34	3.46	Female (df = 13)	-	7.12	0.0001
					Day of inc. (df = 1)	0.05 ± 0.02	4.77	0.07
					Mean recess length (df = 1)	-0.002 ± 0.0007	10.10	0.001
Length of recesses (n = 830)	2.13	0.0008	0.07	41.32	Female (df = 13)	-	2.02	0.02
					Day inc. (df = 1)	1.11 ± 5.56	2.47	0.11
					Female*Day inc. (df = 13)	-	2.68	0.001

[a] Parameter estimate ± 1 S.E.

Figure 2.1. Change in recess frequency with day of incubation and average length of recesses for Northern Shoveler females nesting at Minto Flats, AK.

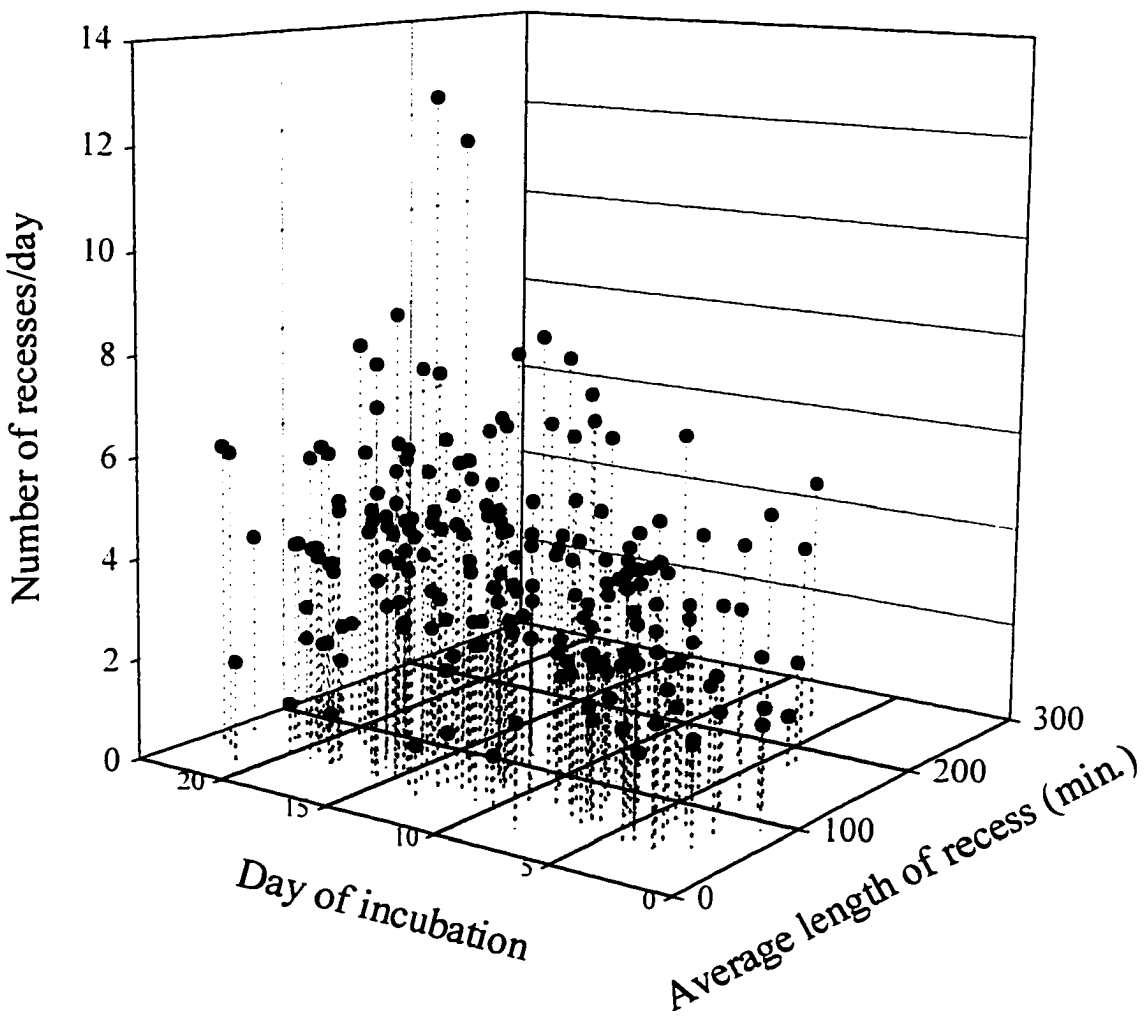
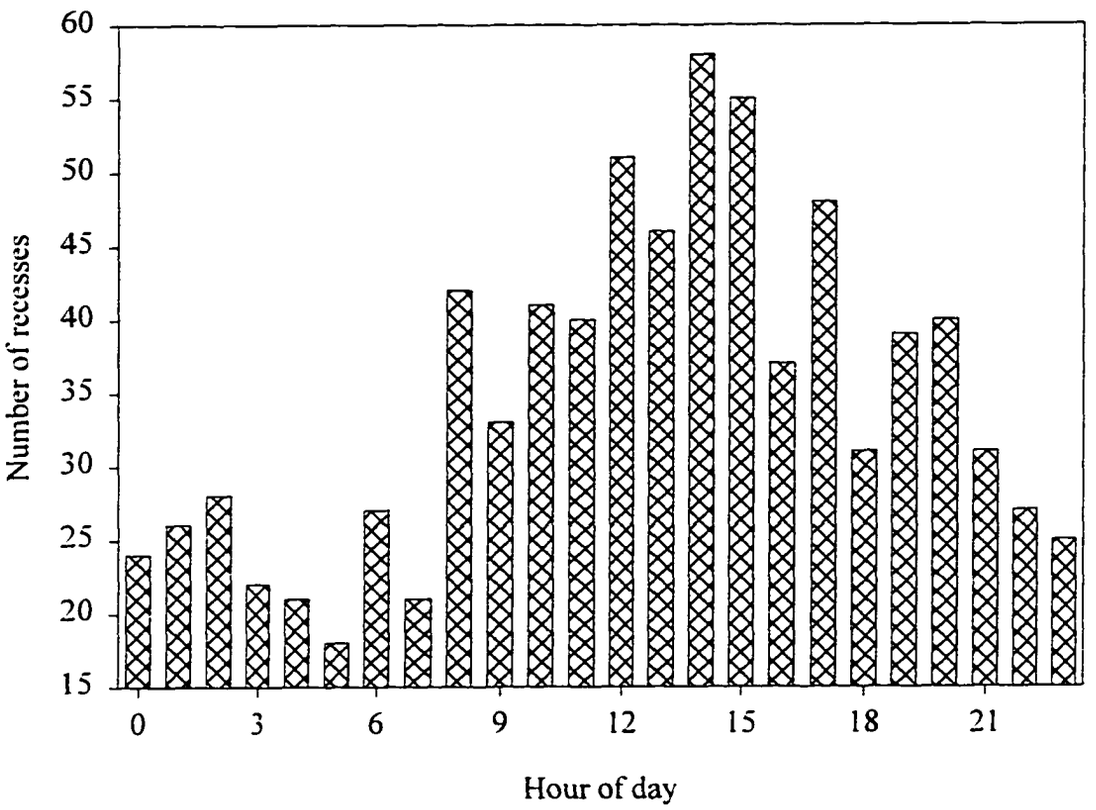


Figure 2.2. Distribution of timing of recesses during the incubation period for 14 female Northern Shovelers nesting at Minto Flats, Alaska (n = 831 recesses).



TRADEOFFS IN ENERGETIC INVESTMENT IN THE CLUTCH AND INCUBATION BY NORTHERN SHOVELERS NESTING AT MINTO FLATS, ALASKA[3]

Abstract. Incubation is an energetically costly process, and conserving energy for incubation could ultimately modify clutch volumes produced by female ducks. We measured female nest attendance during incubation, body weight between successive nest trappings, and clutch volume produced by Northern Shovelers (*Anas clypeata*) in the subarctic during summer 1993. We found no relationship between average daily nest attendance and change in body weight, clutch volume produced, or body size. For a larger sample of birds collected over 3 years of study we evaluated factors influencing clutch volume produced. We found that in relation to clutch volume produced: larger females produced larger clutch volumes, early nesting females produced larger clutch volumes than late nesting females, there was a difference between years in clutch volume produced, and that date affected clutch volume produced by large and small females differently. Our results are consistent with most other studies of ducks, indicating that daily weight loss does of incubating females not affect nest attentiveness. A proximal explanation for our results is microclimate of nests and ambient environmental

---

[3] Prepared for submission to *The Condor* as: MacCluskie, M. C. and J. S. Sedinger. Tradeoffs in Energetic Investment in the Clutch and Incubation by Northern Shovelers Nesting at Minto Flats, AK.

conditions. Lack of a relationship between weight loss and daily nest attendance could be explained by female quality and/or territory quality. Further studies addressing trade-offs between nest attendance, weight loss and clutch volume should simultaneously examine these variables.

Keywords: nest attentiveness, weight loss, Northern Shoveler, Anas clypeata, costs of incubation.

INTRODUCTION

Many species of ducks (Family Anatidae) use endogenous nutrient reserves to produce a clutch (see Alisauskas and Ankney 1992 for review, Mann and Sedinger 1992, Alisauskas and Ankney 1994, Esler and Grand 1994, Gammonley 1995). Because of substantial variation among females in nutrient reserves remaining at the end of egg laying, Ankney and Alisauskas (1991) proposed females may make tradeoffs between energy invested in the clutch and energy used to incubate eggs. While incubating females of several species are in negative energy balance (Ankney and Afton 1988, Afton and Paulus 1992), incubation has not generally been viewed as an energetically limiting event for species in the Tribe Anatini. However, energy could limit incubation capacity if females are in negative energy balance after egg production.

While small body size of most ducks precludes the ability to reduce food intake during incubation as much as geese do (Afton 1980), body reserves are important for ducks during incubation. Endogenous reserves provide 25% of incubation energy

expended by Mallards (*Anas platyrhynchos*) and 16% of energy expended by Northern Shovelers (*Anas clypeata*, hereafter shoveler) nesting in Manitoba (Gloutney and Clark 1991). Using the same equation as Gloutney and Clark (1991), we calculated that endogenous reserves accounted for 29% of incubation energy expended by shovelers nesting in interior Alaska (MacCluskie 1997).

Female ducks are generally in negative energy balance during incubation as declining body mass over the whole incubation period has been reported numerous times (see Afton and Paulus 1992 for review, Mallory and Weatherhead 1993). Gloutney and Clark (1991) found that female Mallards and Shovelers with higher body masses at the end of incubation had higher nesting success than females with lower body masses. However, Gloutney and Clark (1991) did not report volumes of eggs laid by females and did not assess tradeoffs made between investment in clutches and weight loss (Ankney and Alisauskas 1991).

Tradeoffs, if they exist, may be difficult to detect because variation in female quality can create positive correlations among females between investment in clutches and nest attentiveness. Erikstad et al. (1993) examined incubation period, nesting success, body mass, and clutch volume produced by Common Eiders (*Somateria mollissima*) and found that females producing the largest clutches had the shortest incubation periods (indicating highest rates of nest attendance), ended incubation with the highest body masses, and were more successful in hatching young from their nests.

Additionally, Black Brant (*Branta bernicla nigricans*) producing larger clutches were more attentive to nests than females producing smaller clutches (Eichholz 1996). Variation in female quality does not preclude trade-offs by females of comparable quality, but variation in female quality must be controlled in some manner if a tradeoff hypothesis is to be adequately tested.

Shovelers nesting at Minto Flats, Alaska do not use endogenous reserves during egg production, although females use endogenous lipid reserves at a significant rate during incubation (MacCluskie 1997). Additionally, shovelers nesting at Minto Flats are less attentive than conspecifics nesting in mid-continental North America (MacCluskie 1997). We simultaneously measured clutch volume, weight loss and nest attentiveness in a sample of shovelers to examine variation in overall reproductive effort among females and to determine if females producing large clutch volumes were less attentive to their nests during incubation to test for a tradeoff between investment in eggs and investment in incubation.

METHODS

Data were collected during the summers of 1991-1993 on the Minto Flats State Game Refuge (64° 50' N, 148° 50'W), AK (hereafter Minto). See Petrula (1994) and Mann and Sedinger (1992) for detailed descriptions of the study area. Habitat used by nesting shovelers in this wetland complex is meadow dominated by bluejoint grass (*Calamagrostis canadensis*), sedge (*Carex sp.*), and marsh five-finger (*Potentilla*

palustris). Shovelers initiated nests, on average, by 30 May, and the interval between initiation of the first and last nests was 40.0 ± 5.5 (S.D.) days (Petrula 1994). We began field work on 15 May and conducted standard searches for nests (Klett et al. 1986) from 0800 to 1400 hrs. Alaska Daylight Time (ADT). Nests were located when females were flushed from their nests. When nests were found, we determined day of incubation by candling eggs (Weller 1956). Each egg in the nest was individually numbered, and length and width were measured (± 0.1 mm) using vernier calipers. For each female, we calculated date of nest initiation by subtracting the day of incubation and clutch size from the date on which the nest was found.

During the 3 years of the study, we collected females during all stages of incubation from known nests for a separate study of nutrient reserve dynamics during breeding (MacCluskie 1997). Immediately upon collection, we weighed females (±1.0 g) using a Pesola scale and measured culmen length, tarsus length, and wing chord (± 0.1 mm) using vernier calipers. We also measured body length from distal edge of culmen to the distal end of the pygostyle (± 1.0 cm). We calculated clutch volume produced by each female by determining the volume of each egg in the clutch using the formula $0.515*L*W^2$ (mm), where L is egg length and W is width (Hoyt 1979), then summing egg volumes for the clutch.

We monitored nest attendance of a sample of females in 1993 using an artificial egg in each sample nest that recorded female presence/absence and nest air temperature

(Flint and MacCluskie 1995). Artificial eggs were placed in nests as soon as nests were located. Data were recorded on a single-channel data logger and retrieved from data loggers using a portable computer every 6 days. We also monitored ambient temperature at nests using a thermistor probe attached to surrounding vegetation at approximately nest height. At times we flushed females from their nests when we visited nests to retrieve data from dataloggers. Therefore, to remove observer influence from our calculations of nest attendance, we eliminated 2 hours of data recorded after a nest visit.

In 1993 only, a sub-sample of females that were monitored for nest attendance were trapped on their nests in early incubation (about day 10) and weighed, then re-trapped near at the end of incubation (day 20-24) and weighed again. For these females we determined a rate of weight loss/day based on the number of days in between first and second trappings. We also calculated an average percent of day each female spent on her nest during the interval between first and last trapping.

To control for variation associated with body size among females, we calculated a First Principal Components score (PC1) using the 4 morphological measurements taken when females were nest trapped (Alisauskas and Ankney 1987). Thirty-two percent of the variation in morphological data was explained by PC1. We also calculated a standardized date of nest initiation (i.e., the first day an egg was laid in the nest) for each nest to control for annual variation in timing of nest initiation. Standardized date of nest initiation was calculated by determining the date of peak nest initiation for Shovelers in

each year (day 0), and adding or subtracting the number of days after or before the peak that an individual female started nesting.

Statistical Analyses

Initially we analyzed data for the relationship between average nest attentiveness and body weight change using an Analysis of Covariance (ANCOVA), which included the covariates mean daily nest attendance and clutch volume produced by the female; however our sample size was small (n = 7). We also performed a regression of body mass on day of incubation and used those residuals in a multiple regression of nest attentiveness on clutch volume and mass residual.

Cooling rate of nests was determined for females for which we also collected nest attendance data. Cooling rates of clutches are typically calculated as the slope of the relationship between the change in nest air temperature per minute (Y) during a recess from the nest and the difference between the nest air temperature and ambient temperature (X) (Kendeigh 1977). For our sample of birds we modified this approach, using ANCOVA with female as a fixed factor because we wanted to determine if cooling rates of nests varied among females. Among-female variation included variation due to female behavior as well as nest microclimate (e.g., covering nest with down during absences).

To test if females that were heavier at the end of incubation had invested less energy in the clutch we used an ANCOVA model which included clutch volume as the

response variable. Covariates were body mass at the time of collection, body size (PC1), standardized date of nest initiation, and day of incubation; class variables were year and the 2-way interaction of PC1*standardized date of nest initiation. All statistical procedures were performed using the General Linear Models (GLM) procedure in the SAS Statistical Package (SAS Institute, 1990)

RESULTS

During the 3 years of the study, we collected body weight and clutch volume data from 40 incubating females. In 1993, we measured weight loss and nest attentiveness between 2 nest trappings for 7 females. We determined average nest attendance and clutch volume, for 5 additional females in 1993 that we did not weigh. Therefore, sample sizes differ for each analysis because we included all females for which we had appropriate data.

Mean nest attentiveness of females between nest trappings was 72.24 ± 0.12 (S.E.) %. There was no significant relationship between average nest attentiveness and weight loss or clutch volume produced by the female (clutch volume $F_{1,5} = 0.29$, $P = 0.63$; change in weight $F_{1,5} = 0.12$, $P = 0.75$). Body weight actually tended to increase 0.0015 ± 0.004 (S.E.) g for each one percent increase in average attentiveness. Nest attentiveness was not related to clutch volume produced or change in female body mass, adjusted for stage of incubation (clutch volume $F_{1,5} = 1.00$, $P = 0.36$; adjusted mass $F_{1,5} = 1.91$, $P = 0.23$). Average nest attendance during the entire incubation period was not

related to either clutch volume ($F_{1, 12} = 1.05$, $P = 0.32$) or standardized date of nest initiation ($F_{1, 12} = 1.80$, $P = 0.20$) for the 14 females we could include in this analysis.

Nests cooled at a rate of 0.002 ± 0.0006°C/°C/min, which was significantly different from 0 ($F_{1, 126} = 10.6$, $P = 0.002$). Females differed in the rate at which nest air temperature changed ($F_{5, 122} = 3.29$, $P = 0.009$).

Variation in clutch volumes produced during all 3 years of the study ($n = 40$) was explained by body size ($F_{1, 33} = 7.35$, $P = 0.01$), standardized date of nest initiation ($F_{1, 33} = 35.33$, $P = 0.001$), year ($F_{2, 33} = 11.12$, $P < 0.001$), and an interaction between body size and standardized date of nest initiation ($F_{1, 33} = 11.48$, $P = 0.002$) (Fig. 1). Body weight at the time of collection ($F_{1, 33} = 0.57$, $P = 0.45$) and day of incubation ($F_{1, 33} = 0.03$, $P = 0.87$) explained no variation in clutch volume. Females produced 27747.78 mm^3 (or 77% of an average egg) for each unit increase in body size. Clutch volume declined 5346 mm^3 (or 15% of an average egg) for each day later females initiated nests. Mean clutch volume in 1991 was the smallest for all three years of the study, and mean clutch volume in 1992 was smaller than mean clutch volume in 1993 (Table 1). The interaction between body size and standardized date of nest initiation indicates that the effect of date was different on small females than was the effect of date on large females. We calculated the % change in clutch volume produced between small and large females was 7.2 % for a given date.

DISCUSSION

Our data do provide no evidence that female Shovelers nesting in Alaska make tradeoffs between energy invested in clutch volume and energy used for nest attendance during incubation. However, we calculated that our power (Zar 1984) to detect a relationship between clutch volume and nest attentiveness was < 50%, moreover, to have a 95% chance ($P = 0.05$, 2 tailed test) of detecting a relationship between clutch volume and nest attentiveness we would have required a sample size of 46.

However, we might not have expected to detect a tradeoff between clutch volume and nest attendance in our study, even with adequate sample sizes. If females drop below some nutrient threshold to produce a larger clutch volume, the energetic deficit may be erased the first few days after clutch completion if food is abundant. Shovelers nesting at Minto, even when in peak energy demand, do not use endogenous reserves during egg production (MacCluskie 1997), indicating that females, on average, remain in energy balance during egg production. Therefore, this population of shovelers may be a poor one for testing the trade-off hypothesis because an energetic tradeoff is not occurring. Ankney and Alisauskas (1991) originally proposed tradeoffs between investment in the clutch and investment in incubation for populations that relied on stored nutrients during egg laying. Several other studies have documented use of endogenous reserves during egg production (see Alisauskas and Ankney 1992 for review, Mann and Sedinger 1992, Alisauskas and Ankney 1994, Esler and Grand 1994, Gammonley 1995). Therefore clutch volume/nest attentiveness trade-offs may be more easily detected in those

populations.

We are unaware of any other study that has simultaneously examined daily patterns of female weight loss during incubation, volume of clutch produced, and daily nest attendance pattern of the female during incubation. Erikstad et al. (1993) found female Common Eiders that produced larger clutches had higher body masses at the end of incubation and also that heavy females had shorter incubation periods, showing that variation in female quality could influence a nest attentiveness/clutch volume trade-off. Eichholz (1996) found Black Brant (*Branta bernicla nigricans*) females that had invested more in eggs were more attentive to their nests; however, after he controlled for body size, he found no relationship between nest attentiveness and amount of clutch volume produced. Both of these studies support a female quality hypothesis in which large females produce large clutches of large eggs and are more attentive to their nests. After controlling for female weight during egg laying and body size, Eichholz (1996) also found a tradeoff between investment in eggs and nest attentiveness. For females at a given weight at a given stage of incubation, females that invested more in eggs were least attentive to their nests (Eichholz 1996).

We also failed to detect a relationship between daily nest attentiveness and female weight loss, indicating that females that were more attentive did not lose weight more rapidly. In fact, slope of the relationship between nest attentiveness and weight loss, while non-significant, was negative. Such a relationship could occur if the most attentive

females occupied the best territories, allowing them to meet a larger proportion of their energy needs by foraging. Other studies examining this hypothesized relationship, while limited in number, are consistent with our findings: Mallory and Weatherhead (1993) found no relationship between daily mass loss and nest attendance for 3 of 4 Common Goldeneyes (*Bucephala clangula*) studied; Hepp et al. (1990) found no effect of early-incubation body mass on hatching success for Wood Ducks (*Aix sponsa*). While Mallory and Weatherhead (1993) proposed that Goldeneyes mitigated mass loss by adjusting nest attendance, even though their 'data do not provide clear support for it', our data clearly indicate that changes in body weight do not influence nest attentiveness. In the larger sample, for which we knew clutch volume, initiation date, body size, and one body weight, clutch volume and body weight were not related although clutch volume and body size were related. This result supports the hypothesis that larger females produce larger clutch volumes and is consistent with the female quality hypothesis.

Hepp et al. (1990) found a positive relationship between body mass of female wood ducks at the end of incubation and survival to the next breeding season. In contrast, Arnold et al. (1995) found no difference between late incubation body mass of Redheads (*Aythya americana*) or Canvasbacks (*Aythya valisineria*) and survival to the next year, except for yearling Canvasbacks. Lower survival of females with lower weights at the end of incubation suggests the potential for a tradeoff between investment in reproduction and adult survival. Alternatively, our failure to detect either use of nutrient reserves

during egg laying (MacCluskie 1997) or a relationship between female condition and nest attentiveness suggests substantial variation in female quality that influences all aspects of breeding and could also influence survival.

We propose the results of our study and those for Goldeneyes and Wood Ducks may be due, in part, to microclimate of nests and ambient environmental conditions. Cavity nesting species such as Goldeneyes and Wood Ducks (Wilson and Verbeek 1995) do not experience fluctuations in nest temperature that are as dramatic as upland nesting species. For example, Gloutney et al. (1996 b) reported that incubating Mallards and Blue-winged Teal nesting in central Saskatchewan were below the thermal neutral zone (TNZ) 23 and 55% of the time, respectively. Females nesting in cavities may not be constrained to staying on nests to prevent eggs from freezing (Afton and Paulus 1992) or from overheating (Webb 1987), both of which may cause deformity and/or death of embryos (Webb 1987, Afton and Paulus 1992). Shovelers nesting at Minto Flats experience temperatures that are rarely below freezing or above temperatures harmful to embryo development for most of the nesting season (MacCluskie 1997). Our observed cooling rates of nests are approximately half the value Afton (1980) reported for shovelers nesting in Manitoba (0.13 °C/°C/hour from Minto Flats vs. 0.22 °C/°C/hour from Manitoba), which provides further evidence of more benign ambient conditions for females at Minto. Therefore, daily weight loss of adult females could be ameliorated by favorable environmental conditions.

Incubation is a necessary event for successful reproduction in ducks. Females are in negative energy balance (Afton and Paulus 1992, Gloutney et al. 1996a), and costs of incubation increase as clutch volume increases (Weathers 1985, Moreno and Carlson 1989, Moreno et al. 1991, Gloutney 1996b). Thus, costs of incubation must be taken into account in evaluation of factors affecting successful reproduction for waterfowl. We suggest to accurately evaluate evolution of clutch volume in waterfowl, energetic patterns during egg production and daily incubation behavior must simultaneously be considered.

ACKNOWLEDGMENTS

Funding for this study was provided by U.S. Fish and Wildlife Service, Migratory Bird Management, Region 7, Alaska Department of Fish and Game, and Delta Waterfowl and Wetlands Research Station. Logistical support was provided by the Institute of Arctic Biology and Fish and Wildlife Cooperative Research Unit, University of Alaska Fairbanks. We thank John Dunn, Mark Keech, Amy Larsen, and Tim Obritschkewitsch for assisting in data collection. B. Barnes and E. Murphy provided reviews that improved this manuscript.

LITERATURE CITED

AFTON, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82:132-137.

AFTON, A. D., AND S. L. PAULUS. 1992. Incubation and brood care in waterfowl. p. 62-108. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. The ecology and management of breeding waterfowl. University of Minnesota Press. St. Paul.

ALISAUSKAS, R. T. AND C. D. ANKNEY. 1987. Age-related variation in the nutrient reserves of breeding American Coots, *Fulica americana*. Can. J. Zool. 65:2417-2420.

ALISAUSKAS, R. T. and C. D. ANKNEY. 1992. The cost of egg-laying and its relation to nutrient reserves in waterfowl. p. 30 -61. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.]. The ecology and management of breeding waterfowl. University of Minnesota Press. St. Paul.

ALISAUSKAS, R. T. AND C. D. ANKNEY. 1994. Nutrition of breeding female Ruddy Ducks: the role of nutrient reserves. Condor 96:878-897.

ANKNEY, C. D. AND R. T. ALISAUSKAS. 1991. Nutrient-reserve dynamics and diet of breeding female Gadwalls. Condor 93:799-810.

ARNOLD, T. W., M. G. ANDERSON, R. B. EMERY, M. D. SORENSON, AND C. N. DESOBRINO. 1995. The effects of late-incubation body mass on reproductive success and survival of Canvasbacks and Redheads. Condor 97:953-962.

BIEBACH, H. 1984. Effect of clutch size and time of day on the energy expenditure of

incubation starlings (*Sturnus vulgaris*). Physiol. Zool. 57:26-31.

COLEMAN, R. M. AND R. D. WHITTALL. 1988. Clutch size and the cost of incubation in the Bengalese finch (*Lonchura striata* var. *domestica*). Behav. Ecol. Socio-biol. 23:367-372.

EICHHOLZ, M. W. 1996. Body size, individual quality and regulation of incubation in Black Brant. M.S. Thesis, University of Alaska Fairbanks.

ERIKSTAD, K. E., J. O. BUSTNES, AND T. MOUM. 1993. Clutch-size determination in precocial birds: a study of the Common Eider. Auk 110:623-628.

ESLER, D. AND J. B. GRAND. 1994. The role of nutrient reserves for clutch formation by Northern Pintails in Alaska. Condor 96:422-432.

FLINT, P. L. AND M. C. MACCLUSKIE. 1995. A device for simultaneously measuring nest attendance and nest temperature in waterfowl. J. Field Ornithol. 66:515-521.

GAMMONLEY, J. H. 1995. Nutrient reserve and organ dynamics of breeding Cinnamon Teal. Condor 96:985-992.

GATTI, M. 1983. Weight loss in the Mallard. Can. J. Zool. 61:565-569.

GLOUTNEY, M. L. AND R. G. CLARK. 1991. The significance of body mass to female dabbling ducks during late incubation. Condor 93:911-816.

GLOUTNEY, M. L., N. WEST, AND R. G. CLARK. 1996a. Metabolic costs of incubation and clutch size determination in the Red Junglefowl, *Gallus gallus spadiceus*. Comp. Biochem. Physiol. 114A(3):265-270.

GLOUTNEY, M. L. AND R. G. CLARK. 1996b. Clutch size limitation and incubation strategies of birds: responses of ducks to clutch manipulation. *In review*.

HARVEY, W. F. IV, G. R. HEPP, AND R. A. KENNAMER. 1989. Body mass dynamics of Wood Ducks during incubation: individual variation. Can. J. Zool. 67:570-574.

HEPP, G. P., R. A. KENNAMER, AND W. F. HARVEY. 1990. Incubation as a reproductive cost in female Wood Ducks. Auk 107:756-764.

HOYT, D. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73-77.

KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GARILOV. 1977. Avian energetics. Pages 127-204 in J. Pinowski and S.C. Kendeigh [eds.]. Granivorous birds in ecosystems. Cambridge Univ. Press. Cambridge.

KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U. S. Fish and Wildl. Ser. Res. Publ. No. 158. 24 pp.

MACCLUSKIE, M. C. 1997. Proximate control of reproductive effort in Northern Shovelers (Anas clypeata) Nesting at Minto Flats, Alaska. Ph.D. Thesis, University of Alaska Fairbanks, Fairbanks, AK.

MALLORY M. L. AND P. J. WEATHERHEAD. 1993. Incubation rhythms and mass loss of Common Goldeneyes. Condor 95:849-859.

MANN, F. E. AND J. S. SEDINGER. 1993. Nutrient-reserve dynamics and control of clutch

size in Northern Pintails breeding in Alaska. Auk 110:264-278.

MORENO, J., AND A. CARLSON. 1989. Clutch size and the costs of incubation in the Pied Flycatcher (*Ficedula hypoleuca*). Ornis. Scand. 20:123-128.

MORENO, J., L. GUSTAFSSON, A. CARLSON, AND T. PART. 1991. The cost of incubation in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*. Ibis 133:186-193.

MROSOVSKY, N., AND D. F. SHERRY. 1980. Animal anorexias. Science 207:837-842.

PETRULA, M. J. 1994. Nesting ecology of ducks in interior Alaska. M.S. thesis, University of Alaska Fairbanks, Fairbanks.

ROHWER, F. C. 1985. The adaptive sigificance of clutch size in prairie ducks. Auk 102:354-361.

SAS. 1990. SAS user's guide: statisitcs. SAS Institute Inc., Cary, North Carolina. Ver6, 4th Ed.

SHERRY, D. F. 1980. Weight loss and anorexia in birds. J. Comp. Physiol. Psych. 94:89-98.

SWENNEN, C. J., URSEM, C. H. AND P. DUIVEN. 1993. Determinate laying and egg attendance in Common Eiders. Ornis. Scand. 24:48-52.

WEATHERS, W. W. 1985. Energy cost of incubation in the canary. Comp. Biochem. Physiol. 81A:411-413.

WEBB, D. R. 1987. Thermal tolerance of avian embryos: a review. Condor 89:874-898.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. J. Wildl. Manage. 20:111-113.

WILSON, S. F. AND N. A. M. VERBEEK. 1995. Patterns of Wood Duck nest temperatures during egg-laying and incubation. Condor 97:963-969.

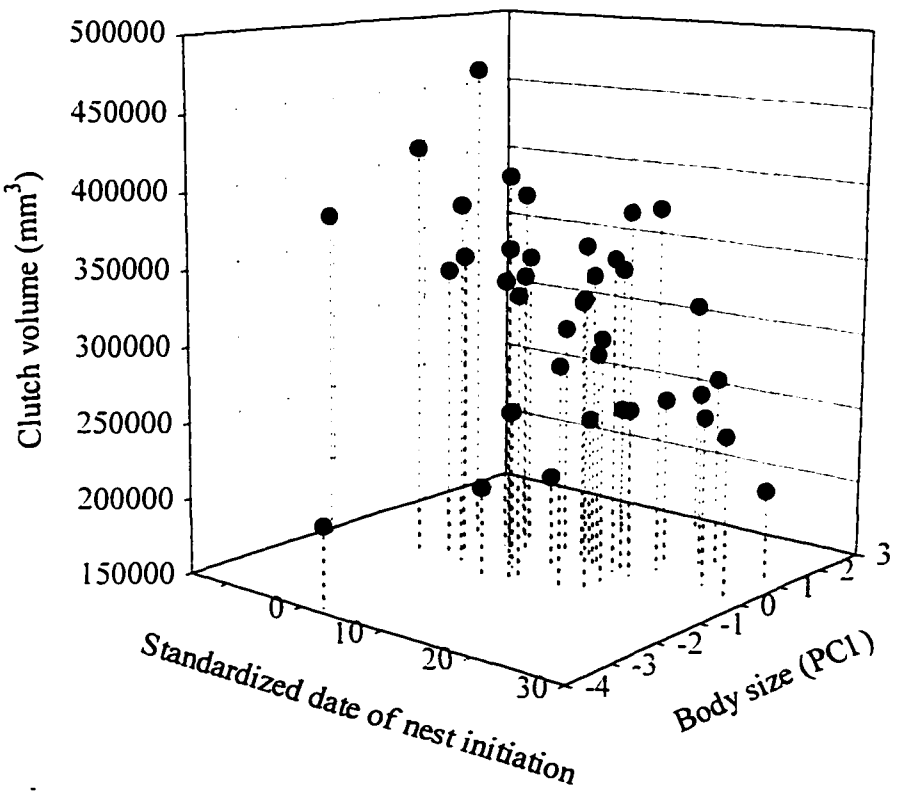
ZAR, J. H. 1984. Biostatistical Analysis. Prentice Hall, London.

Table 3.1. ANCOVA results describing variation in clutch volume produced by female Shovelers during 1991-93 at Minto Flats, AK.

Model								
Dependent variable	***F***	***P***	r^2	**Intercept**	**Source**	**Estimate**	***F***	***P***
Clutch volume (n = 40)	7.81	0.0001	0.63	477203 ± 104826[a]	Weight df = 1	-133.0 ± 176.2	0.57	0.45
					Day of inc. df = 1	238 ± 1480	0.03	0.87
					Body size df = 1	27747± 10236	7.35	0.01
					Day of nest init. df = 1	-5346 ± 899	35.33	0.0001
					Year df = 2	-	11.12	0.0002
					Body size * Day of nest init. df = 1	-3050 ± 900	11.48	0.002

[a] Parameter estimate ± 1 S.E.

Figure 3.1. Relationship of the decline in clutch volume with body size and standardized nest initiation date for 40 females collected during incubation 1991-93 at Minto Flats, AK.



Variation in Incubation Periods and Egg Metabolism in Mallards: Intrinsic Mechanisms to Promote Hatch Synchrony[4]

Abstract. We investigated factors affecting incubation time and metabolic rates of Mallard (*Anas platyrhynchos*) eggs incubated under constant environmental conditions. Time required to reach the star-pipped stage of hatch varied among females ($P = 0.03$), but not with laying sequence ($P = 0.64$) or egg size ($P = 0.25$). Metabolic rate of eggs varied positively with position in the laying sequence ($P = 0.02$) and tended to vary among females ($P = 0.07$). Metabolic rate did not vary with egg volume $r = 0.31$, $P = 0.54$) or incubation length $r = 0.33$, $P = 0.38$). Our results indicate metabolic rate may act as one synchronization mechanism for hatch. The role of maternal effects in development time should be considered in subsequent studies of incubation time in ducks.

Key words: Mallard. Anas platyrhynchos, *metabolism, egg, incubation, incubation length.*

INTRODUCTION

Waterfowl typically begin incubation before the clutch is complete (Caldwell and

---

[4] Published as MacCluskie, M. C., P. L. Flint and J. S. Sedinger. Variation in Incubation Periods and Egg Metabolism: Intrinsic Mechanisms to Promote Hatch Synchrony. The Condor 99:224-228.

Cornwell 1975, Cooper 1978, Afton 1979, Cargill and Cooke 1981, Afton and Paulus 1992), which results in developmental asynchrony of eggs within clutches at the end of laying (Caldwell and Cornwell 1975, Afton 1979, Kennamer et al. 1990). However, asynchrony at hatching is less than that observed at the end of laying (Caldwell and Cornwell 1975, Afton 1979, Cargill and Cooke 1981), suggesting that some mechanisms exist to synchronize hatch (Afton 1979, Davies and Cooke 1983). Such mechanisms could include developmental retardation of eggs laid early in the laying sequence or developmental acceleration of eggs laid after the onset of incubation (Davies and Cooke 1983). In either case eggs incubated in natural conditions must have variable incubation lengths.

Differences in incubation period could be either extrinsic to the egg or intrinsic to the egg. Extrinsic mechanisms could include behavior of the parent. For example, eggs in the center of the nest have higher temperatures (Caldwell and Cornwell 1975), thus females may alter development time of specific eggs by regulating egg position in the nest. Also, vocal stimulation decreases time to hatching (Vince 1966, Orcutt and Orcutt 1976) and may accelerate development of later laid eggs (Davies and Cooke 1983). Intrinsic factors include inherent properties of the egg, such as egg composition, egg size, or physiology. Smaller eggs require less incubation, both among and within species (Worth 1940, Rahn and Ar 1974, Martin and Arnold 1991, Arnold 1993). Martin and Arnold (1991) found effects of egg size on incubation length were relatively weak when

studied within species, however their analysis did not control for among female factors other than egg size. Egg composition also varies among (Alisauskas 1986, Hepp et al. 1987) and within clutches (Alisauskas 1986), which could influence development rate. Alternatively, inherent differences in metabolic rate might result in differences in development time. Several studies have demonstrated greater variation in lipid reserves among newly hatched chicks as compared to freshly laid eggs, suggesting differential lipid reserve use among eggs (Alisauskas 1986, Hepp et al. 1987, Slattery and Alisauskas 1995).

The combination of these studies led us to hypothesize that relationships may exist among metabolic rate, egg size, and the time required for embryo development. Our goal in this study was to examine the potential for among female variation in intrinsic factors to influence egg development in a controlled incubation environment (i.e., incubator), thereby eliminating female behavior as an extrinsic factor. Factors we considered were maternal contribution to eggs, egg size, egg metabolic rates, and egg sequence in the clutch.

METHODS

We conducted this study at the Delta Waterfowl and Wetlands Research Station, Portage la Prairie, Manitoba, Canada from April - July, 1994. Thirty, 1 year-old, captive, wild stock Mallards (*Anas platyrhyncos*) were used for this study. We placed each pair in 2 x 4 m breeding pens on 30 April. All pairs were fed ad libitum Delta Waterfowl Turkey

Starter and had free access to water for bathing and swimming. A covered, wooden box filled with straw was placed in each pen for a nesting structure. Appropriate animal use and care permits were obtained from the Canadian Wildlife Service (Permit# WS-M25), and the University of Alaska Fairbanks (IACUC Protocol # 94-019) for all portions of this study.

Beginning 1 May, nest boxes were checked twice daily for eggs. Nest checks were conducted between 09:00 and 11:00 and again between 18:00 and 20:00. Fresh eggs were removed from the nest and replaced with a plastic egg of similar size, weight and color. Our goal was to remove eggs as soon as possible so that they would be minimally exposed to female behavior. Eggs were individually numbered on the blunt end with an indelible marker and placed in a commercial grade incubator (Humidaire 550) that maintained a constant temperature of 37.5°C and relative humidity of 84-87% . Eggs were assigned random locations in the incubator to randomize microclimate effects. Eggs were candled every 7 days to determine fertility (Weller 1956). Infertile eggs were removed from the incubator, and fertile eggs were replaced in their location.

Development Time

Eggs that were judged to be within 12 hours of initiating hatch, based on candling (Weller 1956), were removed from the incubator and placed in a hatching machine (Humidaire Hatcher 50) that maintained a relative humidity of 87-89% and a temperature of 37.2°C. We assigned eggs to random locations in the hatching machine to randomize

microclimate effects. Eggs in the hatching machine were examined every 8 hours to determine timing of hatch, which we defined as occurring when shells were star-pipped. A star-pipped egg was one for which the shell had cracked enough to create a small diameter circle (approximately 3 mm). We use the star-pipped stage to define hatch because variable humidity in the hatching machine may have artificially increased shell exodus time for some ducklings. The star-pipped stage of hatch is the first externally observable stage of hatch, and was the most unaffected by humidity fluctuations in this study.

Metabolic Measurements

We randomly selected one egg from early, middle and late in the laying sequence of each clutch. Egg position in the laying sequence was determined using all fertile and infertile eggs in a clutch. We measured metabolic rate on these eggs two or three times during the incubation period. Metabolic rates were measured using a closed-system respirometry apparatus consisting of two, 240-ml glass jars, each fitted with an airtight injection port and connected by a manometer filled with colored water (Scholander 1950). One jar served as the chamber to hold the egg, the bottom of which was covered with Ascarite to absorb CO_2 produced by the embryo, while the other jar served as a pressure buffer and completed the closed system. Eggs were placed in the respirometry chamber on a piece of wire mesh 1.5 cm over the Ascarite. Both jars were then placed with the upper 2 cm exposed in a circulating water bath (40°C) which maintained a chamber temperature of

37°C. Lids were placed loosely on jars and we allowed eggs to equilibrate in the apparatus for 10 minutes before beginning a trial. The manometer was not submerged at any time and rested outside the water bath so that water level in the manometer could be monitored. All steps preceding submersion of the chambers were completed as quickly as possible to minimize temperature fluctuations experienced by the egg. After equilibration, the pre-injection level of the manometer was recorded, lids were secured on both chambers and 1 ml of pure, ambient temperature and pressure O_2 was injected into the chamber using a 3 ml gas-tight syringe. The plunger of the syringe was pumped three times after O_2 injection to ensure an even mixture of gas in the chamber. After the third time the plunger was pumped, a stopwatch was started and time required for the manometer level to return to the equilibration point was recorded. Three trials were conducted for each metabolic measurement. Barometric pressure and chamber temperature were recorded at the beginning of each trial and true volume of oxygen (ml) consumed by the embryo was corrected to standard temperature and pressure (STP). Measurements of oxygen consumption were converted to a rate of oxygen consumption, defined as ml of oxygen consumed/hour. Length (L) and width (W) of all eggs were measured to the nearest 0.01mm using vernier calipers and egg volume was calculated as $0.515*LW^2$ following the methods of Hoyt (1979a).

Statistical Analyses

We used analysis of covariance (ANCOVA) to examine variation in incubation length.

We used egg development time (from laying to star pipped) in days as the dependent variable, female and laying sequence (early, middle or late) as class variables, and egg volume as a covariate in the analysis.

We also used ANCOVA to examine variation in metabolic rates of eggs. We used metabolic rate/hour as the dependent variable, female and laying sequence in the clutch as class variables, and egg volume and day of incubation as covariates. Day of incubation was included since metabolic rate varies with stage of incubation in several species of *Anas* (Hoyt et al. 1979b, Vleck and Vleck 1980).

We tested for a direct relationship between development time and metabolic rate using an ANCOVA model that included egg size, metabolic rate, day of incubation, and laying sequence in the clutch. For this analysis, we used days to star-pipped stage of hatching as the response variable and the last metabolic measurements taken from each egg as the independent variable. Day of incubation was a covariate and laying sequence was a class variable in this test. Only eggs that were observed in the star-pipped stage of hatch and had a metabolic rate measurement were used for this analysis.

To determine if metabolic rates of eggs varied with egg volume, we regressed the $\log_{10}$ metabolic rate from the last measurements taken on each egg against $\log_{10}$ egg volume (Ricklefs 1984) while controlling for laying sequence and female effects. We were specifically interested in testing the null hypothesis that the slope of this line would equal 1, indicating isometry. A slope different from 1 would indicate a proportional

increase or decrease in size-specific metabolic rates.

All statistical analyses were conducted using the General Linear Models (GLM) Procedure of the SAS statistical package (SAS Institute 1990). Type III sums of squares were used to evaluate the contribution of individual variables to models for all analyses. A significance level of $P < 0.05$ was used for all tests.

RESULTS

Only 17 of the 30 pairs of Mallards used for the study produced fertile clutches (defined as clutches with at least two viable eggs). Cause of infertility in these 1-year-old birds was unknown, but we suspect inexperience of males and possibly low sperm count (Stunden 1996).

We measured time from laying to star pipped for 49 eggs from 10 females. Average development time from laying to star pipped was 22.5 days (range 20.9-24.4) among females. Egg incubation period varied significantly among females, but not with position in the laying sequence. Likewise incubation period was not significantly related to egg volume, the correlation coefficient was negative (slope = -0.02)(Table 1).

We measured metabolic rates on 45 eggs from 13 females. Egg metabolic rate varied with rank in the laying sequence, tended to vary among females, but did not vary significantly with volume (Table 1). Average egg metabolic rates ($\pm$ SE) for the entire incubation period after controlling for the covariates female, volume and laying sequence were 9.46 ($\pm$ 1.08), 11.09 ($\pm$ 1.07, and 13.24 ($\pm$ 1.07) ml oxygen per hour (STP) for eggs

from early, middle, and late in the laying sequence, respectively (Fig. 1). Day of incubation (Fig. 1) explained a significant amount of variation in metabolic rate (Table 1). Log egg metabolic rate did not increase significantly with log egg volume (slope = 0.578, 95% CI = -1.33 - 2.48, r =0.31, P=0.54).

We detected no relationship between time to reach star pipped stage of hatch and metabolic rate ($F_{1,14}$ = 0.79, P = 0.38), egg volume ($F_{1,14}$ = 1.10, P = 0.31), day of incubation ($F_{1,14}$= 0.40, P = 0.53), or position in the clutch ($F_{2,14}$ = 0.20, P = 0.81); our sample size was only 20 eggs for this analysis, however.

DISCUSSION

The goal of our study was to determine if, after removing female behavioral effects, there was an intrinsic mechanism influencing egg incubation period. We found no relationship between intrinsic variables we measured and incubation length within clutches. However, our data suggest that variation in egg metabolic rate is one mechanism by which hatch synchrony occurs because late sequence eggs tended to have higher metabolic rates. Therefore, in a natural setting intrinsic factors may be important to, and work in concert with, extrinsic factors to promote hatch synchrony, but not in this study because of the experimental design.

We also hypothesized that within females, intraclutch variation in egg size may be an adaptation to synchronize hatch (Flint and Sedinger 1992, Arnold 1993, Flint et al. 1994) and specifically, that late laid eggs would be smaller and require less incubation

time. Our data do not support this hypothesis however, because egg size explained an insignificant proportion of variation in egg development time and metabolic rate. Small sample size reduced our power to detect a relationship between egg size and development time.

Variation in egg metabolism may represent a trade-off between lipid used during development and amount of lipid reserves remaining at hatch. For example, high egg metabolism would result in faster embryo development and slower egg cooling rate, but fewer lipid reserves would remain at hatch. This could be important because small lipid reserves at hatch may influence early juvenile survival (Ankney 1980). Alisauskas (1986) showed that rate of lipid metabolism varied among eggs for American Coots (*Fulica americana*) and Hepp et al. (1987) suggest a similar result for Wood Ducks (*Aix sponsa*). Additionally, Slattery and Alisauskas (1995) showed that metabolism of lipid stores did not increase isometrically with egg size (but see Rhymer 1988). Our finding that egg metabolism did not increase isometrically with egg size is consistent with their results. We believe that lipid use by embryos during development is likely correlated with egg metabolism. The mechanism by which metabolic rates of eggs vary with respect to laying sequence is unknown.

Egg metabolic rate was not directly linked to incubation length in our data set. One explanation for this may be that late sequence eggs, while having higher metabolic rates, would hatch at a relatively less mature condition. Other studies have shown

variation among hatchlings in tissue water content (Ricklefs 1984, Alisauskas 1986) and related that to tissue maturity. We did not account for this variation in our study. Therefore, we recommend controlling for tissue water content of hatchlings in subsequent studies.

We observed significant variation in incubation period among females. Similarly, Arnold (pers. comm. reanalysis of Arnold et al. 1993) also found significant variation among females in length of incubation of wild Blue-winged Teal (*Anas discors*) but detected no among female variation in incubation length in Mallards and Northern Shovelers (*Anas clypeata*). The risk of nest predation should favor shorter incubation period for females (Arnold et al. 1987). There may, however, be costs associated with shorter incubation length if eggs hatch with reduced lipid reserves as a result (see above).

To our knowledge, this study is the first that has attempted to control for maternal behavioral and genetic effects on egg development time and metabolic rate in wild-strain ducks. We detected significant variation in length of the incubation period and metabolic rate of eggs among females. Our data suggest higher metabolic rates in later laid eggs may aid in synchronization of hatch in ducks. Overall, our findings indicate that the maternal component of eggs should be considered when examining questions involving incubation aspects of life history of the Anatidae.

ACKNOWLEDGMENTS

Funding for this project was provided by Delta Waterfowl and Wetlands Research Station. We thank Julie Campbell, Lea Craig, Dean Jeske, and Kim Wright for assistance collecting data. We would also like to thank the staff of Delta Waterfowl and Wetlands Research Station for logistical support. Todd Arnold, Frank Rohwer and Brian Barnes provided valuable reviews that greatly improved this manuscript.

LITERATURE CITED

AFTON, A. D. 1979. Incubation temperatures of the Northern Shoveler. Can. J. Zool. 57:1052-1056.

AFTON, A. D., and S. L. PAULUS. 1992. Incubation and brood care. In B. Batt, A. Afton, M. Anderson, C. D. Ankney, D. Johnson, J. Kadlec, G. Krapu [eds.], Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis.

ALISAUSKAS, R. T. 1986. Variation in the composition of the eggs and chicks of American Coots. Condor 88:84-90.

ANKNEY, C. D. 1980. Egg weight, survival, and growth of Lesser Snow Goose goslings. J. Wildl. Manage. 44:174-182.

ARNOLD, T. W., F. C. ROHWER, and T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. Am. Nat. 130:643-653.

ARNOLD, T. W. 1993. Factors affecting egg viability and incubation time in prairie

ducks. Can. J. Zool. 71:1146-1152.

BATT, B. D. J., and G. W. CORNWELL. 1972. The effects of cold on Mallard embryos. J. Wildl. Manage. 36:745-751.

CALDWELL, P. J., and G. W. CORNWELL. 1975. Incubation behavior and temperatures of the mallard duck. Auk 92: 706-731.

CAREY, C. 1983. Structure and function of avian eggs. Current Ornithology. 1:69-102.

CARGILL, S. M., and F. COOKE. 1981. Correlation of laying and hatching sequences in clutches of the Lesser Snow Goose (*Anser caerulescens caerulescens*). Can. J. Zool. 59:1201-1204.

COOPER, J. A. 1978. The history and breeding biology of the Canada Goose of Marshy Point, Manitoba. Wildl. Monogr. No. 61.

DAVIES, J. C., and F. COOKE. 1983. Intra-clutch hatch synchronization in the Lesser Snow Goose. Can. J. Zool. 61:1398-1401.

FLINT, P. L., LINDBERG, M. S., MACCLUSKIE, M. C. and J. S. SEDINGER. 1994. The adaptive significance of hatching synchrony of waterfowl eggs. Wildfowl 45:248-254.

FLINT, P. L., and J. S. SEDINGER. 1992. Reproductive implications of egg size variation in Black Brant. Auk 109:896-903.

HEPP, G. R., D. J. STANGOHR, L. A. BAKER, and R. A. KENNAMER. 1987. Factors affecting variation in the egg and duckling components of Wood Ducks. Auk

104:435-443.

HOYT, D. F. 1979a. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73-77.

HOYT, D. F., BOARD, R. G., RAHN, H. and C. V. PAGANELLI. 1979b. The eggs of the Anatidae: conductance, pore structure, and metabolism. Physiol. Zool. 52:438-50.

KENNAMER, R. A., W. F. HARVEY, and G. R. HEPP. 1990. Embryonic development and nest attentiveness of Wood Ducks during laying. Condor 92:587-592.

MARTIN, P. A., and T. W. ARNOLD. 1991. Relationships among fresh mass, incubation time, and water loss in Japanese Quail eggs. Condor 93:28-37.

ORCUTT, F. S. Jr., and A. B. ORCUTT. 1976. Nesting and parental behavior in domestic Common Quail. Auk 93:135-141.

PAGANELLI, C. V., ACKERMAN, R. A., and H. RAHN. 1978. The avian egg: In vivo conductances to oxygen, carbon dioxide, and water vapor in late development, pp. 212-218 *in* J. Piiper [ed.], Respiratory function in birds, adult and embryonic. Springer-Verlag, Berlin.

RAHN, H., and A. AR. 1974. The avian egg: incubation time and water loss. Condor 76:147-152.

RHYMER, J. M. 1988. The effect of egg size variability on thermoregulation of Mallard (*Anas platyrhynchos*) offspring and its implications for survival. Oecologia

75:20-24.

RICKLEFS, R. E. 1984. Variation in the size and composition of eggs of the European starling. Condor 86:1-6.

SAS INSTITUTE, INC. 1985. SAS User's Guide: statistics. Ver. 5. SAS Institute, Inc. Cary, NC.

SCHOLANDER, P. F. 1950. Volumetric plastic micro respirometer. Rev. Sci. Instruments. 13:32-33.

SLATTERY, S. M. and R. T. ALISAUSKAS. 1995. Egg characteristics and body reserves of the neonate Ross' and Lesser Snow Goose. Condor 97:970-984.

STUNDEN, C. E. 1996. Studies on reproductive characteristics and artificial insemination in captive Mallard ducks (*Anas platyrhyncos*). MS thesis. University of British Columbia.

TULLET, S. G. 1975. Regulation of avian eggshell porosity. J. Zool. 177:338-348.

VINCE, M. A. 1966. Artificial acceleration of hatching in quail embryos. Anim. Behav. 14:389-394.

VLECK, C. M. and D. VLECK. 1980. Patterns of metabolism and growth in avian embryos. Amer. Zool. 20:405-416.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. J. Wildl. Manage. 20:111-113.

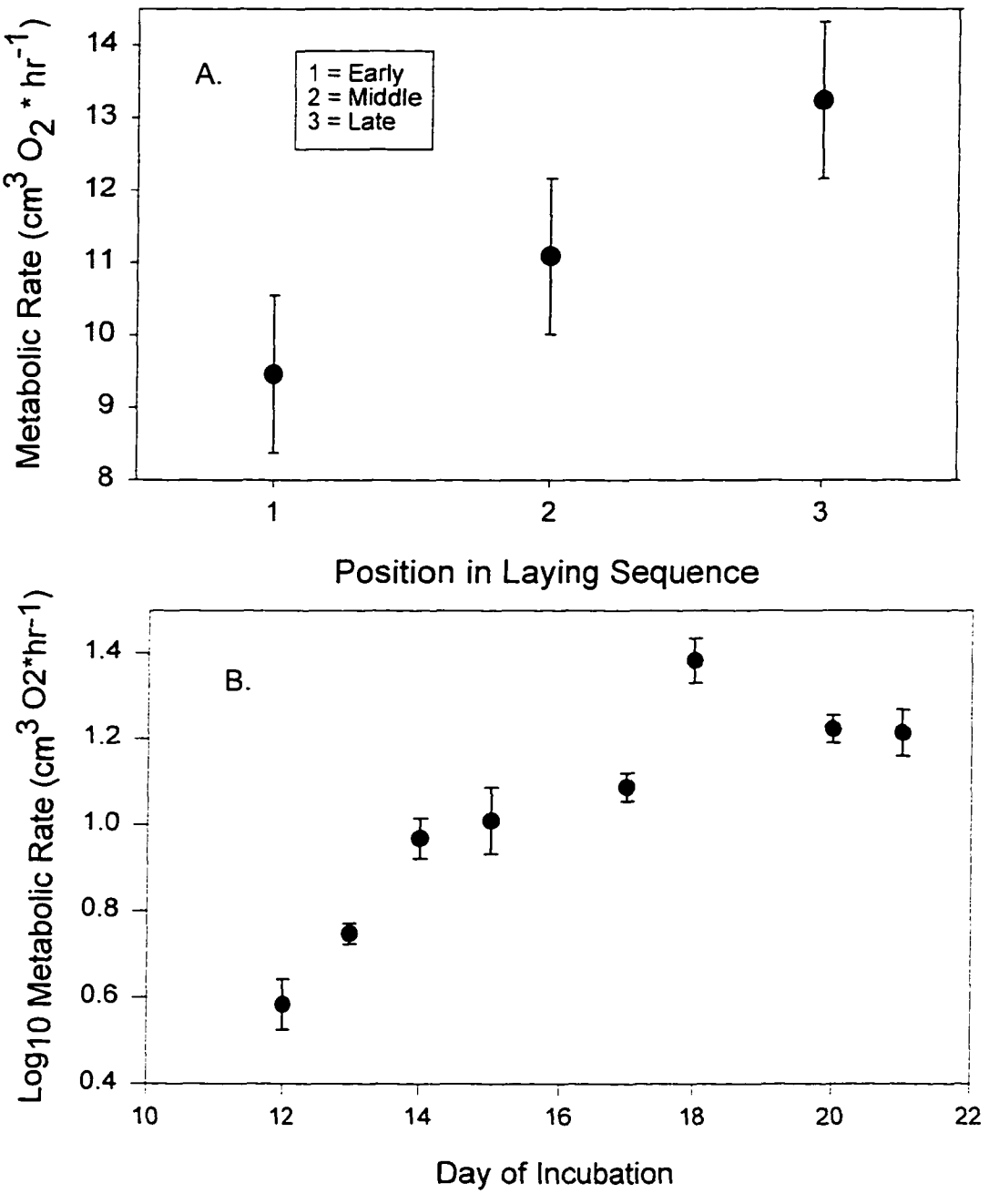
WORTH, B. C. 1940. Egg volumes and incubation periods. Auk 57:44-60.

Table 4.1. General linear models describing variation in egg development time and metabolic rate for mallard eggs.

Egg development time (n=49)	df	F	P
Female	9	2.26	0.03
Laying sequence	2	0.12	0.88
Egg volume	1	1.24	0.27

Egg metabolic rate (n=45)	df	F	P
Female	12	1.98	0.07
Laying sequence	2	4.63	0.02
Egg volume	1	0.24	0.63
Day of incubation	1	18.95	<0.001

Figure 4.1. A. Mean metabolic rate of eggs early, middle and late in the laying sequence. Points for each position in laying sequence (n = 45) are mean rates of all eggs within each category ± 1 SE. B. Mean change in metabolic rate of Mallard eggs during incubation. Points for each day of incubation (n = 42) are mean rates of all eggs from all females ± 1 SE.



OVERALL CONCLUSIONS

Nutrient Reserve Dynamics and Reproductive Investment: Female shovelers nesting at Minto Flats do not use somatic nutrient reserves to produce eggs. This pattern differs markedly from data reported from the prairies where female shovelers store somatic protein and use somatic lipid during laying to produce a clutch. However, females from Minto and the prairies exhibit similar patterns of somatic lipid reserve use during incubation. Minto females may be proximally limited during incubation by the size of somatic lipid reserves. Changes in organ weights and intestine lengths are similar for females at Minto and females from the prairies.

My results could be explained by several hypotheses. Food availability is likely similar between Minto and Manitoba; thus, coupled with long days, females at Minto may be able to remain in energy balance during egg production. I observed females nesting at Minto were larger in body size than females breeding in Manitoba. Because body reserves are proportional to body size, but metabolic rate increases with body size to the 0.734 power, larger females are capable of potentially having larger lipid reserves and longer fasting endurance. This means that large females from Minto could realize an energetic benefit during reproduction because they are larger.

Females at Minto may make seasonal tradeoffs with regard to reproduction. Delay of nest initiation may result in increased food availability for females; however, ducklings may survive less well if nest initiation is delayed such that ducklings hatch

after peak food abundance. My data are inconsistent with a hypothesis that clutch size is proximally limited by nutrient availability during egg production because nutrient reserves did not decline during laying.

Nest Attendance Patterns and Tradeoffs in Energetic Investment: Patterns of nest attendance exhibited by females at Minto were different than those exhibited by females nesting in Manitoba. Females at Minto were less attentive and took more recesses each day that were of longer duration females in Manitoba. These results indicate that food may be in short supply during incubation because females did not use endogenous reserves to produce eggs; however, they used endogenous lipid at a significant rate during incubation. Yet, Minto females did not appear to make energetic tradeoffs between energy they invested clutches and energy devoted to incubation of clutches. There was no relationship between nest attendance, change in body weight, clutch volume produced, or body size. These results were consistent with most other studies of ducks, indicating that daily weight loss of the female during incubation does not affect nest attentiveness. Proximal explanations for my observations are microclimate of nests and ambient environmental conditions at Minto. Lack of a relationship between weight loss and daily nest attendance could be explained by variation in female quality and/or territory quality.

Variation in Incubation Periods and Egg Metabolism: Variation in egg metabolic rate is one mechanism that may which synchronize hatch within clutches because eggs produced

late in the laying sequence tend to have higher metabolic rates. Variation in egg metabolism may cause a tradeoff between lipid used during embryo development and amount of lipid reserves remaining at hatch. however small lipid reserves at hatch may influence early juvenile survival. Egg metabolic rate was not directly linked to incubation length. however this result could be explained if eggs produced late in the laying sequence hatch in a relatively less mature condition.

Overall this research provides little support for proximal limitation of reproductive effort of female shovelers nesting at Minto Flats. With the exception of lipid reserve use during incubation. females do not use body reserves during reproduction. which differs from results for shovelers nesting in Manitoba. To determine if these results are due to a geographical difference or if shovelers at Minto Flats are anomalous with regard to other species nesting there. further comparative work of other species nesting in the prairies and a species nesting at Minto Flats is required.